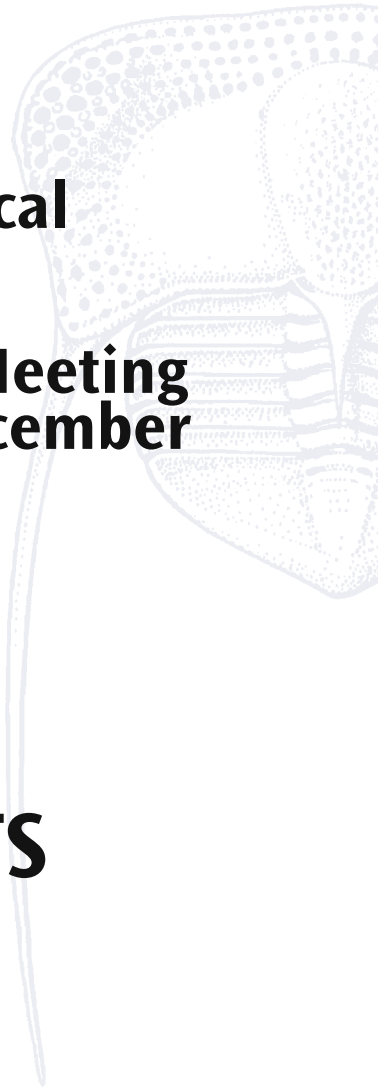
The Palaeontological Association

46th Annual Meeting 15th–18th December 2002

University of Cambridge

ABSTRACTS



Oral presentations

Oral presentations will take place in the Physiology Lecture Theatre and, for the parallel sessions at 11:00–1:00, in the Tilley Lecture Theatre. Each presentation will run for a maximum of 15 minutes, including questions. Those presentations marked with an asterisk (*) are being considered for the President's Award (best oral presentation by a member of the Palaeontological Association under the age of thirty).

Timetable for oral presentations

MONDAY 9:00

Affinity of the earliest bilaterian embryos
Xiping Dong and Philip Donoghue

Calamari catastrophe
Philip Wilby, John Hudson, Roy Clements and Neville Hollingworth

Tantalizing fragments of the earliest land plants
Charles H. Wellman

Use of Morphometrics to Identify Character States
Norman MacLeod

Constructional Morphology of Pelagic Crinoids
Adolf Seilacher and Rolf B. Hauff

Origins of teeth amongst jawed stem group gnathostomes
Moya Meredith Smith and Zerina Johanson

MONDAY 11:00—Marine Palaeontology A (parallel)

***Growth patterns in primitive hexactinellid sponges**
Joseph P. Botting

Ichnology of the type area of the Maastrichtian Stage (Upper Cretaceous): burrowing and boring immediately prior to the K/T boundary event
Stephen K. Donovan and John W.M. Jagt

Phytoplankton diversity and distribution patterns in the Triassic: the dinoflagellate cysts of the upper Rhaetian Koessen Beds (Northern Calcareous Alps, Austria)
Susanne Feist-Burkhardt, Björn Holstein and Annette E. Götz

A new Locality for *Schizocystis armeta* (Forbes, 1848)
William Fone and Christopher R.C. Paul

***Cornulites serpularius*—pursuing a Palaeozoic enigma**
Liam Herringshaw

The evolutionary diversification of Palaeozoic echinoids
Charlotte Jeffery

Holocene reef structure and growth at Mavra Litharia, southern coast of Gulf of Corinth, Greece: a simple reef with a complex message
Steve Kershaw and Li Guo

New perspectives in palaeoscolecidans
Oliver Lehnert and Petr Kraft

MONDAY 11:00—Non-marine Palaeontology A (parallel)

Guts and Gizzard Stones, Unusual Preservation in Scottish Middle Devonian Fishes
R.G. Davidson and N.H. Trewin

***The use of ichnofossils as a tool for high-resolution palaeoenvironmental analysis in a lower Old Red Sandstone sequence (late Silurian Ringerike Group, Oslo Region, Norway)**
Neil Davies

The harvestman fossil record
Jason A. Dunlop

A New Trigonotarbid Arachnid from the Early Devonian Windyfield Chert, Rhynie, Aberdeenshire, Scotland
Steve R. Fayers and Nigel H. Trewin

***Molecular preservation of upper Miocene fossil leaves from the Ardeche, France: implications for kerogen formation**
S. Neal Gupta, A. Stott, D.E.G. Briggs, R.P. Evershed and R.D. Pancost

***A new archaeopteridalean progymnosperm from Venezuela**
Susan Hammond

***Responses of paratropical vegetation over different time scales to climate changes in the Palaeogene**
Guy Harrington

Bone invasion: Microbial focal destruction in Late Miocene mammal bone
George Iliopoulos

MONDAY 2:00—Precambrian/Cambrian A

Early diagenesis in a Lower Cambrian black shale: more than meets the eye
Uwe Balthasar

Signs of life in a desiccating, dysaerobic, upper Middle Cambrian lagoon
Nicholas J. Butterfield

***Census fossil assemblages from the Middle Cambrian Burgess Shale**
Jean-Bernard Caron

***Hallucigenia* unveiled**
Desmond Collins

The dawn of deuterostome evolution: red sky in morning, calcichordates warning?
Simon Conway Morris and Degan Shu

Palaeoecological distribution of Ediacaran fossils
Dima Grazhdankin

MONDAY 4:00—Precambrian/Cambrian B

***Halkieriids in Middle Cambrian phosphatic limestones from Australia**
Susannah M. Porter

Body building in *Halkieria* and comparisons with chitons and other possible stem-group molluscs
Bruce Runnegar

***The Early Cambrian *Mickwitzia* from Greenland and Nevada and the origin of the brachiopods**
Christian Skovsted, Lars E. Holmer and Alwyn Williams

***Waptia fieldensis*, a possible crustacean from the Middle Cambrian Burgess Shale of British Columbia, Canada**
Rod S. Taylor and Desmond H. Collins

Cambrian food chains: new perspectives
Jean Vannier, Chen Junyuan, Zhu Maoyan and Huang Diying

The origin of metazoan reefs: Neoproterzoic of the Nama Group, Namibia
Rachel Wood, John P. Grotzinger and J.A.D. Dickson

TUESDAY 9:00—Extinctions and Transitions

***Oceanographic changes during the Late Devonian mass extinction**
David Bond

The palaeoclimatic significance of the Devonian-Carboniferous boundary
J.E.A. Marshall, T.R. Astin, F. Evans and J. Almond

***A Global Overview of the lundgreni (Wenlock, Silurian) Graptoloid Extinction Event**
Lucy Muir

***Microfaunas across the Bathonian-Callovian boundary**
K.J. Riddington

Significance of a recently discovered, exceptionally diverse, Early Triassic marine assemblage from Oman
Richard J. Twitchett

The end-Permian mass extinction: sudden or gradual?
Paul B. Wignall

TUESDAY 11:00—Marine Palaeontology B (parallel)

Hydrothermal vent and cold seep molluscs: view from the fossil record
Crispin T.S. Little and Kathleen A. Campbell

The morphology of hyolithids and its functional implications
Mónica Martí Mus and Jan Bergström

Microplankton associations and biofacies: testing Silurian palaeoenvironmental models
Gary L. Mullins, Richard J. Aldridge and David J. Siveter

A revised high-resolution ammonite time scale for the Lower Jurassic of Great Britain
Kevin N. Page

Palaeobiology of Carboniferous microcrinoids
George Sevastopulo

Composition, depositional setting and palaeoecology of Siphonodendron biostromes in the late Viséan of SE Ireland
Ian D. Somerville and P. Cózar

***Calcareous nannofossil assemblages during the Messinian Salinity Crisis: evidence from the Polemi Basin, Cyprus**
Bridget S. Wade and Paul R. Bown

Early ontogenetic development of blastoids
Johnny A. Waters and Sara A. Marcus

TUESDAY 11:00—Non-marine Palaeontology B (parallel)

The Middle Devonian Flora of Yunnan, China
Christopher M. Berry and Wang Yi

***How to make dinosaur tracks: interpreting dinosaur footprint formation and preservation using laboratory controlled simulations**
Simon Jackson

***Application of high-resolution computed tomography in palaeontology: analysis of a Middle Devonian labyrinthodont tooth from New York State, USA**
Vicky MacEwan

***The influence of substrate consistency on footprint morphology: field experiments with an emu**
Jesper Milàn and Richard G. Bromley

The cranial morphology and systematics of the enigmatic basal ornithischian Heterodontosaurus tucki Crompton and Charig, 1962
David B. Norman, Alfred W. Crompton and Alan J. Charig

Ancient weavers on the silk road: Jurassic spiders from China
Paul Selden and Dong Ren

***Microevolution of the charophyte genus *Harrisichara* across the Eocene-Oligocene transition in the Isle of Wight, Southern England**
Nick P. Sille, Michal Kucera, Margaret E. Collinson and Jerry J. Hooker

***Trackways meet trackmakers: the composition of early tetrapod communities**
Lauren Tucker

TUESDAY 2:00—Palaeoecology

***Tooth wear in Sticklebacks and the role of competition in speciation**
David C. Baines, Mark A. Purnell and Paul J.B. Hart

***Response of Late Carboniferous tropical vegetation to transgressive-regressive rhythms at Joggins, Nova Scotia**
H.J. Falcon-Lang

Relating Sedimentological Context to Ecological Strategy: a method for examining disturbance in the fossil record
Walton A. Green and Dana Royer

***Mid Cretaceous fossil forests from Alexander Island, Antarctica**
Jodie Howe

The evolution of swimming among ammonoids
Christian Klug and Dieter Korn

Walking with Millipedes: Kinematics of Locomotion in Polyxenus and Implications for Reconstructing the Functional Morphology of the Palaeozoic Millipede Arthropleura
Heather M. Wilson

TUESDAY 4:00—Concepts and Approaches

Paedomorphism in the Late Devonian tetrapod Ichthyostega from East Greenland
Henning Blom

Variation in trilobite terrace ridge patterns using extended eigenshape analysis
Abigail Brown and Norman MacLeod

Character concepts in arthropods: new perspectives for bridging morphological disparity
Ruth Ann Dewel, Jetta Eibye-Jacobsen, Muriel Walker and Richard H. Thomas

***Marine invertebrate calcium carbonate—same old story?**
Jennifer K. England, Maggie Cusack and Martin Lee

Phylogenetic Congruence Between Hard and Soft Part Data Sets: How Taphonomy Affects Ostracod Phylogenies
Lisa E. Park

***Conodonts, cladistics and the fossil record**
Linda M. Wickström

Abstracts of oral presentations

*Tooth wear in Sticklebacks and the role of competition in speciation

David C. Baines[1], Mark A. Purnell[1] and Paul J.B. Hart[2]
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Some of the most exciting and widely cited recent work on the ecological controls on speciation focuses on members of the *Gasterosteus aculeatus* species complex. In Canadian lakes, these sticklebacks occur as two morphologically distinct forms or species, and experimental evidence indicates that the differences between them are the result of competition for food resources causing ecological character displacement. The role of competition in evolution is contentious, however, largely because of the fundamental difficulty of extrapolating from field or laboratory experimental results to the longer periods over which new species evolve. The hypothesis that speciation was caused by ecological character displacement driven by trophic niche differentiation is particularly difficult to test in fossils because feeding cannot be observed directly. Functional changes have to be inferred from changes in morphology, and determining whether morphological changes were caused by shifts in feeding thus becomes circular.

Analysis of tooth wear patterns offers a way out of this impasse. Wear on teeth, whether in living or extinct animals, provides direct evidence of tooth use and feeding habits. We have conducted quantitative analysis of tooth wear in laboratory populations of sticklebacks raised under controlled feeding regimes. This is the first quantitative analysis of microwear in non-tetrapods, and our results have important implications for understanding the role of niche differentiation in the evolution of fossil sticklebacks, and in aquatic vertebrates more generally.

Early diagenesis in a Lower Cambrian black shale: more than meets the eye

Uwe Balthasar
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Cathodoluminescence and backscattered SEM analysis of shale-hosted organophosphatic and trilobitic fossils from the Lower Cambrian Mural Formation (Jasper National Park, Canadian Rocky Mountains) reveal a complex early diagenetic history leading to aluminosilicate replacement. In organophosphatic shells, aluminosilicate crystals initiate within the shell along originally organic lamellae of a few microns thickness. In the early stage of replacement these lamellae can be replicated with high fidelity, but during further diagenesis idiomorphic crystals initiate along these lamellae, penetrate the juxtaposed phosphatic layers, and thus destroy the original microstructure. Additionally, a prominent layer of silica occurs frequently at the interior edge of organophosphatic shells, which is often followed by a phosphatic zone up to one millimetre thick, typically with needle shaped aluminosilicate crystals floating in the matrix. Trilobite cuticles are pervasively replaced by aluminosilicates growing as idiomorphic crystals perpendicular to the surface of the cuticle, thereby destroying the primary calcitic shell

microstructure. Reworked specimens of trilobites and organophosphatic fossils in co-occurring limestones also show initial stages of aluminosilicate replacement, indicating its very early diagenetic occurrence. Insofar as these shelly remains co-occur with a range of Burgess Shale-type fossils, this study may shed light on the exceptional preservation seen in the Burgess Shale and Soom Shale, both of which have been reported as resulting from aluminosilicate replacement.

The Middle Devonian Flora of Yunnan, China

Christopher M. Berry[1] and Wang Yi[2]
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[2] Nanjing Institute of Geology and Palaeontology, Academica Sinica, Nanjing, China **<ywangngs@hotmail.com>**

The Middle Devonian Flora of Yunnan was first studied by Halle in 1936. Since then the few publications devoted to these plants have included monographs on large collections of individual plants or small amounts of diverse taxa from scattered localities. We are building up large collections from the Xichong Formation and its lateral equivalents, in order to understand better the nature of the flora as a whole as well as to provide monographic treatments of the individual plants. Floras of Middle Devonian age from Europe, North and South America are dominated by herbaceous lycopsids of widespread distribution, cladoxylopsids, progymnosperms and iridopteridaleans in various proportions. Yunnan assemblages contain endemic herbaceous lycopsids and a moderate sized tree with very conspicuous terminal cones. The presence of cladoxylopsids, progymnosperms and iridopteridaleans has not been confirmed, but rather there are a number of unusual, sometimes large plants which so far defy classification into the normal Middle Devonian groups. The palaeogeographical and evolutionary significance of this flora will be discussed. The assemblages are likely to be as dramatic for our understanding of early plant evolution as some of the other well publicised fossils that have emerged from China in recent years.

Paedomorphism in the Late Devonian tetrapod *Ichthyostega* from East Greenland

Henning Blom
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In the fossil record, analysis of paedomorphism—considered to be an important mechanism of evolutionary change—relies on the understanding and description of interrelationship, change in size and shape, and distribution. Partial growth series from two species of the Famennian (Late Devonian) tetrapod *Ichthyostega* from East Greenland allows comparison of two ontogenetic paths in skull and jaw morphology. Analysis of skull proportions shows that the *Ichthyostega* specimens from the younger Britta Dal Formation have proportionally broader skulls than those of the older Aina Dal Formation. Together with sculpture characters,

proportions have been used to separate these assemblages to two different species. Also the individual ontogenetic growth series are different and show that the juveniles of each species are more similar in proportions than the adults, suggesting that the stratigraphically younger *I. eigili* retained some juvenile characteristics of the stratigraphically older *I. stensioei*. Growth patterns and tooth differentiation in the upper and lower jaws also provide strong support for the hypothesis that *I. eigili* is paedomorphic. This suggests that paedomorphism may have played an important role in the evolutionary experimentation of structure, function and ecology that took place during the fish-tetrapod transition.

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*Oceanographic changes during the Late Devonian mass extinction

David Bond
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The extinctions at the Frasnian-Famennian boundary constitute one of the "big 5" crises of the fossil record. Numerous causes have been proposed for this mass extinction event including meteorite impact and global cooling. The extinction interval is associated with two organic-rich limestone beds, called Kellwasser beds, in the condensed, deep-water German boundary sections: consequently, marine anoxia has also been proposed as a cause of the extinction. Evidence for the global nature of the Kellwasser events has been sought in Late Devonian sections from Poland, France, Belgium and the United States using integrated techniques of pyrite framboid assay, gamma-ray spectrometry and traditional facies analysis. These reveal that only the Upper Kellwasser Horizon, of terminal Frasnian age, may record a truly global oceanic anoxic event. The manifestation of this event varies according to location. In basinal locations anoxic-dysoxic deposition was persistent throughout much of the Frasnian with an intensification of anoxia to truly euxinic conditions occurring at the end of the Stage. In platform interiors and slope settings the anoxic event is a discrete pulse that punctuated oxic background conditions. The oxygenation changes have also been compared with the fossil record, particularly of the styliolinids, an enigmatic group of small, conical-shelled fossils that were probably planktonic. This group persisted in reasonable abundance until the very end of the Frasnian, but their reported persistence into the Famennian has yet to be confirmed.

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*Growth patterns in primitive hexactinellid sponges

Joseph P. Botting
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Detailed studies of the growth patterns of modern siliceous sponges are restricted to demosponges and theoretical models. It is generally assumed that sponge growth is essentially incremental, with completion of one arbitrary unit being followed by external addition. All recent species are thick-walled, but Lower Palaeozoic sponges are dominated by thin-walled hexactinellids, the earliest groups consisting of a single spicule layer. Large populations of a primitive dictyospongiid from the Caradoc of Mid Wales have allowed the reconstruction of

the growth patterns of its spicules and body morphology. The results indicate that growth occurred through continuous expansion of the globose body, accompanied by continuous enlargement of existing spicules, with a spicule size limit being reached only during the lifetime of a few individuals. One implication of this system is that the perfect quadruled pattern of Protospongia, which is only known from specimens of very large size, could have resulted from the enlargement of a species which has tractose development in its early growth stages, or, alternatively, the tractose taxa evolved from quadruled ancestors through paedomorphosis. This variation in spicule size and tract development should therefore be seriously considered when employed for taxonomic purposes.

Variation in trilobite terrace ridge patterns using extended eigenshape analysis

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Many trilobites have cuesta-like structures, known as terrace ridges, on both the dorsal and ventral surfaces of the exoskeleton. These structures are relatively poorly studied and their function is controversial. Although terrace ridges all appear to have the same basic construction, they are highly variable and several types are known, including long, continuous forms with asymmetric profiles running subparallel to the margin and symmetrical forms which bear a qualitative similarity to fingerprints.

Research is underway investigating terrace ridge shape variation across the class Trilobita, using a recently developed morphometric technique, extended (landmark-registered) eigenshape analysis (MacLeod, 1999). Major trends in the variation of simplified terrace ridge arrays are currently being explored, both within and between the terrace ridge-bearing orders. Preliminary results show that analysis of pygidial doublural terrace ridge arrays gives good taxonomic separation and can differentiate both phylogenetically and ecologically coherent groups. In particular, this analysis appears to separate pelagic and benthic terrace ridge-bearing forms, potentially providing an independent morphological test for trilobite mode of life hypotheses based on other aspects of morphology.

Signs of life in a desiccating, dysaerobic, upper Middle Cambrian lagoon

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An extensively mud-cracked black shale unit near the top of the upper Middle Cambrian (Bolaspidella zone) Pika Formation in Jasper National Park, Alberta, Canada, contains diverse range organic-walled microfossils and locally abundant patches of faecal pellets. The microfossils include Wiwaxia sclerites, both simple and jointed(?) polychaete-type chaetae, and

an eclectic assortment of spinose elements. These latter include short curved spines, usually with associated denticles and a subtending elongate pore (poison gland?), longer curved spines with a distinct basal attachment structure (broadly reminiscent of chaetognath grasping elements), and a highly variable array of triangular, setose, and occasionally paired sclerites. It is not clear whether these spinose elements are components of a single taxon; most, however are reliably interpreted as the scalids of priapulid worms. Priapulids are unusually well represented in Burgess Shale-type assemblages, a pattern sometimes interpreted as characteristic of level-bottom ecosystems in the Cambrian. A more likely explanation, however, is found in the unique capacity of living priapulids to withstand relatively extreme dysaerobic and anoxic conditions. Insofar as dysaerobic/anoxic conditions are necessary (though certainly not sufficient) for Burgess Shale-type preservation, it is unlikely that Burgess Shale-type biotas represent "typical" Cambrian communities.

***Census fossil assemblages from the Middle Cambrian Burgess Shale**

Jean-Bernard Caron
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A preliminary assessment of 20 fossil assemblages from the Middle Cambrian Burgess Shale has yielded more than 50,000 specimens, mostly of soft-bodied organisms. Royal Ontario Museum field parties collected the specimens from a series of discrete siliciclastic units in a section extending stratigraphically down through about 5 metres beneath the base of the Phyllopod Bed (Walcott Quarry) on Fossil Ridge. The assemblages include 95 of the genera known previously from the Phyllopod Bed, and at least 35 potential new genera representing a range of phyla. Despite variations in number of species and abundance of specimens, most individual fossil assemblages appear to retain high fidelity to the composition of the source community and represent potential census assemblages. Recurrence of species associations suggests seasonal, or shorter, episodes of burial, and provides an opportunity to study the natural temporal variation of the composition and structure of Burgess Shale communities at an ecologically meaningful scale. The application of multivariate statistical methods to the analysis and interpretation of the variations in these assemblages allows the integration and summary of large numbers of specimens and taxa, thereby providing a means of examining community associations.

***Hallucigenia* unveiled**

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Since Conway Morris named and redescribed *Hallucigenia sparsa* (Walcott, 1911) in 1977, it has been regarded as the weirdest of the Middle Cambrian Burgess Shale animals. Conway Morris' interpretation of the paired spines as legs, with a single row of bifid tentacles along the back, and with a globular head, began a topsy turvy succession of restorations: Ramsköld and Hou in 1991 turned *Hallucigenia* upside down, with the spines along the back; in 1992 Ramsköld

discovered claws from the second row of tentacles on the holotype, and turned *Hallucigenia* front to back, with the head at the narrow end; then, in 1995 Hou and Bergström returned *Hallucigenia* back to front, and revived the globular head of Conway Morris.

Examination of the original and newly collected specimens indicates that there are two different forms of *Hallucigenia*: a larger form with a robust, rigid trunk, a robust neck and a globular head; and a smaller form with a thinner, more flexible trunk, and a small head with two fang-like projections, two short horns and possibly a pair of eyes, connected to the trunk by a very thin neck. Both forms have seven pairs of robust spines along the back, and seven pairs of long, thin, flexible legs terminating in the large claw typical of onychophorans. The two forms may be either sexual dimorphs, or separate *Hallucigenia* species.

The dawn of deuterostome evolution: red sky in morning, calcichordates warning?

Simon Conway Morris[1] and Degan Shu[2]
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In contrast to our understanding of the early evolution of the ecdysozoans and lophotrochozoans, where the fossil record and molecular biology appear to be in fair agreement, the case for the deuterostomes is less resolved. Insights from the Chengjiang Lagerstätte, South China, however, may help in both defining and linking the otherwise notably disparate phyla. Here we report on two interesting discoveries; one confirmatory, the other controversial. The former concerns the discovery of an extensive suite of the fish *Haikouichthys*, hitherto known only from a single and incomplete specimen. The new material confirms its agnathan status, both with respect to the sensory apparatus and also key post-cranial features. The latter concerns a new yunnanozoan, a group with a chequered history in terms of phylogenetic placement. Here we present new evidence that casts serious doubt on the craniate hypothesis, and suggests a position as a stem-group deuterostome of broadly hemichordate grade. New information on the gills suggests that the evolution of the diagnostic pharyngeal openings may have been more complex than hitherto suspected. In addition the new material strengthens a proposed link to the vetulicolians. Chengjiang deuterostomes therefore provide historical data on body-plans that are in accordance with both Romer's somato-visceral hypothesis and Jefferies' calcichordates, specifically with respect to a bipartite body, the anterior of which bears pharyngeal openings and the posterior of which is segmented.

Guts and Gizzard Stones, Unusual Preservation in Scottish Middle Devonian Fishes

R.G. Davidson and N.H. Trewin
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Relics of internal organs identified as kidney, liver, heart, ?spleen, and also eyes, have been recognised in several fish specimens from the Middle Devonian nodule bed localities of Tynet Burn, Gamrie and Lethan Bar, north-east Scotland. Internal organs are represented by dark red to black stains positioned where the organs were situated in life. This phenomenon has been observed in the acanthodians *Diplacanthus, Cheiracanthus* and *Mesacanthus*, and in the actinopterygian, *Cheirolepis*. In some specimens eyes are also preserved as dark stains.

The fossil bone of the fish in nodules from Tynet Burn is stained by iron oxide deposited by the action of chemotrophic bacteria during early burial. Concentration of iron deposition at haemoglobin rich organ sites in early diagenesis may provide the visible contrast which enables traces of these organs to be seen.

Two specimens of the Arthrodire *Coccosteus* display a fusiform mass of stomach contents, containing pebbles that acted as 'gizzard' stones and also fragmentary acanthodian material, providing dietary evidence for this predator.

***The use of ichnofossils as a tool for high-resolution palaeoenvironmental analysis in a lower Old Red Sandstone sequence (late Silurian Ringerike Group, Oslo Region, Norway)**

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The late Silurian Ringerike Group of southern Norway is an early Old Red Sandstone megasequence that marks the regressive culmination of Cambro-Silurian marine deposition in the Oslo Region. It has traditionally been divided into three formations—the Sundvollen and Stubdal Formations to the north of Oslo (representing muddy coastal plain and braided fluvial deposition respectively), and the Holmestrand Formation to the south (representing fluvio-deltaic deposition). A comprehensive ichnological analysis of the Ringerike Group has resolved many problems in the interpretation of the stratigraphical and palaeoenvironmental relationship between the northernmost and southernmost outcrop areas. To the north, various facies dependent ichnoassemblages are dominated by epifaunal arthropod trackways, with less abundant burrows, looping traces, escape structures, and ichnofossils of uncertain origin. In contrast, the Holmestrand Formation has more diverse ichnoassemblages dominated by burrow traces and arthropod resting traces, with less abundant arthropod trackways, escape structures, and looping traces. Other biogenic structures present in both areas include microbial matgrounds, medusoid imprints, and problematic impressions. The distribution of the ichnofauna in each area is clearly facies controlled and provides new insights into both the ichnological subdivision of nearshore environments and the variation in the palaeoenvironmental conditions of the Oslo Region during the latest Silurian.

Character concepts in arthropods: new perspectives for bridging morphological disparity

Ruth Ann Dewel[1], Jetta Eibye-Jacobsen[2], Muriel Walker[3] and Richard H. Thomas[4]

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The task of identifying phylogenetically useful characters for analyses combining fossil and extant taxa is difficult. Complex transformations can greatly modify characters and impede our ability to recognize homology across large gaps of time. The objective of this study was to examine living and fossil arthropods to determine if structures previously thought to be unrelated may actually represent different states of a drastically transformed character. Several characters of ecdysozoans, encompassing such prominent attributes of the Cambrian arthropod fauna as the "Peytoia", frontal appendage, and biramous limb appear to fall into this category. Attention was paid to finding in living arthropods the homologues of characters present in Cambrian arthropods, many of which belong to the stem groups of extant forms. Putative homologues of these characters and others were assessed by standard criteria to identify primary homology. Criteria were relaxed for some characters, which were described with explicit *a priori* statements of putative homology. More broadly defined characters or characters comprised of new structurally and/or functionally discrete states were incorporated with characters from other analyses of ecdysozoans into a phylogenetic analysis using PAUP. The impact of the newly interpreted characters was substantial and yielded unexpected results including a lack of support for such widely accepted taxa as Mandibulata and Myriapoda.

Affinity of the earliest bilaterian embryos

Xiping Dong[1] and Philip Donoghue[2]

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Classical attempts at unravelling the evolutionary history of metazoans have focused upon the early development of living organisms as an absolute guide to evolutionary relationships. Unfortunately, because the fossil record has been limited largely to the remains of adults and late juvenile stages it has had little to offer in this endeavour and, as a result, some of the basic assumptions of evolutionary embryology have escaped testing. Recent discoveries of fossil embryos from the terminal Neoproterozoic of China and Early Cambrian of Siberia provide the potential for such tests but, until the affinity of these embryos can be constrained further, their significance is mute.

New collections of embryos from the Middle and Late Cambrian of China, and Lower Ordovician of North America, include developmental stages from late cleavage through to much later developmental stages in which phylogenetically informative aspects of the organism's anatomy have begun to unfold. The embryos resemble strongly *Markuelia secunda*, described previously by Bengston & Zhao (1997, *Science* **277**: 1645-8), thus providing constraint over the affinity of these, the earliest unequivocal bilaterian embryos. *Markuelia* is a priapulid that underwent direct-development, a life history strategy rare amongst living priapulids. Phylogenetic analysis unequivocally resolves *Markuelia* as a stem-group priapulid and character optimisation suggests that the majority of fossil (stem group) were direct-developers.

Ichnology of the type area of the Maastrichtian Stage (Upper Cretaceous): burrowing and boring immediately prior to the K/T boundary event

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The Vaals, Gulpen and Maastricht formations (Campanian-Maastrichtian) of The Netherlands and Belgium have yielded an ichnofauna comprised of at least 33 ichnogenera of invertebrate burrows and macroborings, many of which still await formal documentation. These structures are indicative of a range of activities in various biotopes immediately prior to the K/T event, and give at least some indication of the presence of taxa lost due to poor preservation of unmineralised and aragonitic skeletons. Some recent discoveries add interesting and tantalizing ichnotaxa to an already diverse list. Enigmatic *Arachnostega gastrochaenae* Bertling in the internal mould of a bivalve represents unusual preservation of a burrow—or is it a boring? An unnamed 'chambered' boring in an oyster shell has a morphology strongly influenced by shell structure. *Radulichnus* Voigt, *Renichnus* Mayoral and *Centrichnus* Bromley and Martinell are three distinctive borings indicative of specific activities of benthic molluscs. Large, non-penetrative *Oichnus* isp. nov. borings infest irregular echinoids, and are distinctive in having concave walls and a large central boss. Internal blisters show that this infestation occurred when the echinoids were alive. Overall, the ichnotaxonomic composition of these formations is as reminiscent of a Cenozoic succession as one from the Mesozoic.

The harvestman fossil record

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Harvestmen (Arachnida: Opiliones) are relatively rare as fossils, but current data on their fossil record is summarised here and superimposed on the most recently published phylogeny—(Cyphophthalmi (Eupnoi (Dyspnoi + Laniatores)))—to infer minimum times for cladogenesis.

The 'primitive' cyphophthalmids lack a fossil record, and thus express a ghost range of c. 400 million years. Fossils potentially referable to the familiar, long-legged eupnoid group occur in the Devonian of the Rhynie chert. Fossils assigned to the Carboniferous arachnid order Kustarachnida are simply misidentified eupnoid harvestmen. Putative members of the more cryptic dyspnoid harvestmen occur in the Carboniferous Coal Measures. The bizarre, spiny, mostly tropical laniatores are only known from Tertiary ambers (mostly Dominican) and thus express a c. 250 million year ghost range. The other major conclusion to be drawn is the relative modernity of almost all the fossil harvestmen. The earliest examples resemble living forms in gross morphology and most Tertiary fossils can be referred to extant genera. This implies an extraordinary degree of stasis within Opiliones throughout their evolutionary history.

***Marine invertebrate calcium carbonate—same old story?**

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Biominerals perform a range of functions in nature and contribute greatly to the fossil record. Calcium carbonate is abundant in invertebrate systems and occurs in a wide range of ultrastructural forms as well as different polymorphs. Two species of living brachiopod, *Terebratulina retusa* and *Neocrania anomala* and the common mussel, *Mytilus edulis*, span a range of ultrastructural motifs as well as two calcium carbonate polymorphs; calcite and aragonite. The valves of *T. retusa* have a primary layer of acicular calcite underlain by calcite fibres of the secondary layer. The dorsal valves of *N. anomala* also have a primary layer of acicular calcite while the secondary layer consists of semi-nacre i.e. tabular calcite that grows by screw dislocations. *M. edulis* valves consist of an outer layer of prismatic calcite with a nacreous aragonite inner layer. Comparison of the major and trace elements as well as the amino acid composition of the three marine invertebrates allows an initial survey of the inorganic and organic components. This will begin to determine the extent to which similar processes have evolved to produce apparently different biominerals.

***Response of Late Carboniferous tropical vegetation to transgressive-regressive rhythms at Joggins, Nova Scotia**

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Fossil plant assemblages are described in their sequence stratigraphic context from the Upper Carboniferous (Langsettian) Joggins Formation of Nova Scotia to elucidate ecosystem response to transgressive-regressive rhythms. Results show that rising base-level resulted in retrograding submerged mires co-dominated by *Lepidodendron* and *Lepidophloios* lycopsids, which were subsequently replaced by short-lived *Paralycopodites* lycopsid communities following mire drowning. Extensive brackish bays existed during early highstand, distally fringed by progymnospermous and gymnospermous coastal/upland vegetation. Late highstand bay

filling generated prograding distributary wetlands dominated by flood-disturbed lycopsid-pteridosperm-sphenopsid communities and cordaite mangroves. As base-level fell, well-drained alluvial plains were dominated by fire-prone cordaite and/or *Sigillaria* communities, which persisted until the next phase of base-level rise resulted in a return to lycopsid-dominated coastal mires. Rhythmic ecosystem succession of this kind repeatedly occurred on a 100-500 ka timescale at Joggins. This is the first time ecosystem response to Late Carboniferous global change has been identified, a process which may have been very important in creating and maintaining high tropical biodiversity.

A New Trigonotarbid Arachnid from the Early Devonian Windyfield Chert, Rhynie, Aberdeenshire, Scotland

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A new trigonotarbid arachnid is introduced from the Early Devonian (Pragian) Windyfield chert. The material comprises an almost complete, exceptionally preserved individual approximately 8mm in length, and fragmentary remains. The specimens occur in bacterially laminated chert. The box-like carapace has a projecting apically toothed clypeus displaying parallel ridges. Both lateral and median eye tubercles are present. The carapace surface has a distinctive lobation and is tuberculate. The lateral and posterior margins appear rebordered. The sternum is indented with a straight posterior margin. The ornament of the walking legs comprises longitudinal rows of thorn-like tubercles. The abdominal tergites and their lateral margins are tuberculate, and the ninth tergite is fused. The sternites exhibit tuberculation along their posterior borders, though laterally the tuberculate ornamentation hints at the presence of fused, relic lateral plates. Although similar in overall body plan, this new arthropod is quite distinct from *Palaeocharinus*, the common trigonotarbid of the Rhynie chert, in both its size and ornamentation. This animal is a palaeocharinid, although similarities may be tentatively drawn with the anthracomartids. Like the other Rhynie chert trigonotarbids, this animal appears to have been a terrestrial predator, and its discovery increases the faunal diversity of this remarkable deposit.

Phytoplankton diversity and distribution patterns in the Triassic: the dinoflagellate cysts of the upper Rhaetian Koessen Beds (Northern Calcareous Alps, Austria)

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The first unequivocal dinoflagellate cysts are known from the Upper Triassic, but the first relatively diverse assemblages in Europe occur in the uppermost Triassic, the Rhaetian. These assemblages are characterised by only a few species and genera belonging to many different families. The dinoflagellate cyst assemblages of the Koessen Beds from a key section in the Calcareous Alps (Eiberg section near Kufstein, Austria) are presented. Most samples are rich in well-preserved dinoflagellate cysts. For the first time, the species *Wanneria listeri* (Stover & Helby 1987) Below 1987, which was so far known only from the Norian of Australia and Indonesia, is recorded from European sediments. The dinoflagellate cyst assemblages change significantly in their quantitative and qualitative composition depending on the lithology of the samples and the position of samples in a sedimentary sequence. The observed distribution patterns are discussed in context with the cyclic sedimentation of the limestones and marls of the Koessen Beds. Moreover, we try to decipher the palaeoecological factors that are responsible for the distribution patterns recognised in the Rhaetian of the Northern Calcareous Alps.

A new Locality for *Schizocystis armeta* (Forbes, 1848)

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Cystoids of the Echinoencrinitidae are known from the Silurian rocks of Britain. However, with the exception of a small number of specimens, locality details are vague or absent for the material available to study. Newly collected samples of *Schizocystis armata* (Forbes, 1848) provide material whose exact provenance is known. A comprehensive review of the British Silurian cystoids has concluded that water depth restricted the distribution of the fauna (Paul, 1967). The British Silurian cystoid material is rare and only available in old collections. Old museum collections seldom record exact locality or horizon of specimens. The Holcroft collection in the Department of Geology, University of Birmingham is an exception. Holcroft was one of the few Victorian collectors to record exact localities. However the localities are no longer available for modern study. We report a new locality in Shropshire yielding articulated specimens of *Schizocystis armata* (Forbes, 1848) together with a rich benthic and nektic fauna that includes crinoids, trilobites, brachiopods and gastropods. The associated fauna provides insight to the lifestyle of the cystoids and the bio-facies they occupied.

Palaeoecological distribution of Ediacaran fossils

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A siliciclastic succession of the late Neoproterozoic Vendian complex, White Sea area, north-western Russia, demonstrates a wide range of sedimentary facies, some of them recurring in a vertical succession. Each lithofacies contains a distinct and separate assemblage of Ediacaran fossils preserved in life position. Facies-controlled distribution also characterizes other Ediacaran localities, so demonstrating for the first time that fossil assemblages occurring in similar facies are directly comparable at a global scale. Thus to a truly remarkable degree the Ediacaran biotas preserved in proximal prodelta settings in South Australia, in the White Sea area, and in Central Urals are closely parallel. The fossil assemblages found globally in fluviomarine facies are also directly comparable, as corroborated by a recent discovery of *Rangea* in a distributary-mouth bar lithofacies in the White Sea area. This in turn reveals a marked degree of environmental sensitivity and pronounced ecological specialization in these early communities. Based on the White Sea section, correspondence between depositional environment and taxonomic composition rules out hypotheses of biogeographic provinciality of the Ediacaran biotas, and also casts doubt on existence of evolutionary progression during Ediacaran times. What is evident is that Ediacaran organisms rapidly explored various environmental settings, ranging from shallow-water deltaic sandy shoals to deep-water aprons, and maintained this ecological disparity, with limited overall change, for more than 20 million years.

Relating Sedimentological Context to Ecological Strategy: a method for examining disturbance in the fossil record

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Too frequently, methods of analysis used by modern ecologists cannot be applied to ancient ecosystems because data of the right type or of sufficiently high quality are not obtainable from the fossil record. One such method is Grime's (1974) procedure for ordinating herbaceous plants in a ternary diagram in which the vertices represent three primary ecological strategies for sessile organisms (Competitor, Stress Tolerator, Ruderal). Here we suggest a method of plotting plant species on similar ternary diagrams based not on their morphology and physiology but on geographic or sedimentological contexts in which they are found. This will allow comparison of the ecological strategies employed by plants in modern and ancient terrestrial ecosystems and

can potentially be generalized to marine ecosystems dominated by sessile organisms in which disturbance is an important factor.

Work cited: Grime, J.P. 1974. Vegetation classification by reference to strategies. *Nature* **250**:2631.

***Molecular preservation of upper Miocene fossil leaves from the Ardeche, France: implications for kerogen formation**

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Organic diagenesis is an important mechanism in fossilisation. Here we report the results of an investigation of the upper Miocene freshwater diatomite of St. Bauzile, which yields diverse plants and arthropods. All the fossil leaves irrespective of plant type show characteristic alkane/alkene peaks (the pyrolysis product of an aliphatic macropolymer) ranging from C-8 to C-33, as well as lignin products and prist-1-enes and prist-2-enes. Polysaccharide and protein moieties were not detected but some samples provide the first reliable demonstration of cutin in fossil leaves. The beetles also yield an aliphatic signature and chitin and protein are absent. No resistant aliphatic macropolymer is present in the extant analogues of several of our samples including conifer needles, oak leaves and beetles. Thus the macromolecular composition of the fossils must be the result of diagenesis. It is clear that short chain aliphatic compounds, with or without other constituents, condense into a macromolecule of cross-linked n-alkyl units with carbon chain lengths up to at least C-33. This mechanism has been referred to as the *in-situ polymerisation model*. The striking similarity between pyrolysates of plant and arthropod fossils and kerogens (the dominant sedimentary organic matter) suggests that *in-situ polymerisation* is important in kerogen formation.

***A new archaeopteridalean progymnosperm from Venezuela**

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Coalified compressions of new archaeopteridaleans were collected from the lowermost Upper Devonian Campo Chico Formation, Sierra de Perijá, Venezuela. The spectacularly preserved specimens made up of branching axes and leaves initially appear two-dimensional like extant fern fronds, but are probably leafy branches of an early tree. *Archaeopteris* itself was originally classified as a fern based on its planated fronds, and only recently has its three-dimensional nature been documented. Morphologically this has put the genus much closer to *Svalbardia,* another archaeopteridalean, which has always been known to have spirally arranged axes but has more deeply dissected leaves than *Archaeopteris*. This study has demonstrated a three-dimensional structure of the new archaeopteridaleans and leaf morphology more or less intermediate between *Svalbardia* and *Archaeopteris*. Clearly the morphology of the Venezuelan plant is similar to that of both *Archaeopteris* and *Svalbardia* indicating its archaeopteridalean nature. The fertile parts closely resemble *A. fissilis/S. polymorpha,* vegetative leaves share

characteristics with *A. sphenofillifolia* and *A. macilenta,* and there is an indication of leaf dimorphism as seen on *A. roemeriana*. It is anticipated that further morphological comparisons, especially with archaeopteridaleans, will lead to a better understanding of the Venezuelan plant's affinities and its place in evolution.

***Responses of paratropical vegetation over different time scales to climate changes in the Palaeogene**

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Understanding the response of vegetation to climate changes on time scales from $10^6 - 10^4$ years is central to many hypotheses on speciation and predictions on future vegetation change. This is especially the case in greenhouse climates that Quaternary vegetation reconstructions are poorly equipped to model. Pollen and spore data from >240 samples are presented here from the eastern US Gulf Coast (palaeo-latitude c. 32° N) that span an interval of c. 3 my and are centred on the Palaeocene–Eocene boundary (54.93 ma). The vegetation type is paratropical throughout and the climate (MAT c. 27°C) was probably comparable to parts of the present-day Amazon basin. The sampling resolution varies considerably but a section near the Palaeocene-Eocene boundary is sampled every 4-8 ky and spans c. 250 ky. Changes in vegetation reveal a probable eccentricity cycle, that is statistically significant through power spectral analysis, but chord analyses show the actual change in vegetation is slight and noted only by a change in abundance of myricaceous pollen. Overall, chord analyses demonstrate that vegetation composition is affected far more strongly over $10^5 - 10^6$ years by secular climate change such as warming throughout the late Palaeocene, additional warming across the Palaeocene–Eocene thermal maximum (PETM) and cooling in the early Eocene.

***_Cornulites serpularius_—pursuing a Palaeozoic enigma**

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The Much Wenlock Limestone Formation (Silurian) of the English Midlands and Welsh Borderlands has yielded more than 650 species of exquisitely preserved fossils. The vast majority can be placed in extant phyla, but a number of problematica remain. One of the most abundant and distinctive, yet least understood, is *Cornulites serpularius* Schlotheim, 1820. *C. serpularius* is a calcareous, annulated, tube-dwelling organism, and the type species of a group that has received various systematic assignations, the most persistent being with the polychaete annelids. However, its characteristics have never been satisfactorily described, such that the diagnosis of other tubular, calcareous fossils as cornulitids is cast into doubt. A comprehensive reassessment of *C. serpularius* has been carried out, revealing shell structures that have not previously been described. These features enable comparison with other purported cornulitids and provide new insights into the biological affinities and functional morphology of both *C. serpularius* and the group as a whole.

*Mid Cretaceous fossil forests from Alexander Island, Antarctica

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Spectacular fossil forests are preserved in mid Cretaceous rocks on Alexander Island, Antarctic Peninsula. Fossil trees and shrubs are preserved within fossil soils in their original positions of growth, within a sequence of river channel sands and floodplain sands and silts. Statistical analysis of the fossil plant data reveals that certain types of plants always occurred together. Three plant assemblages were identified: i) a conifer/fern assemblage with mature conifers of mainly araucarian type and an understory of *Sphenopteris* ferns, ii) a mixed conifer, fern and cycad assemblage with araucarian conifers and *Ginkgo* trees, iii) a disturbance flora of liverworts, *Taenopteris* shrubs, ferns and angiosperms. These plant assemblages were also statistically coupled to specific fluvial environments. Areas near river channels that were frequently flooded by silt-bearing flood waters were colonised by a flora of pioneer species and early colonisers, such as angiosperms, liverworts and ferns, plants that became established quickly and reproduced rapidly. Areas further from the river channels were colonised by more mature vegetation of conifers that were flooded only intermittently so that the large trees were not disturbed.

Bone invasion: Microbial focal destruction in Late Miocene mammal bone

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The taphonomic investigation of Upper Miocene (MN 11-12) fossil mammal bones from Kerassia (Euboea Island, Greece) was undertaken on material from seven different sites near Kerassia, where at least two fossiliferous horizons occur. Polished thin sections of fossil bone and teeth from both horizons of Kerassia and, for comparison, eight other Late Miocene Greek localities were studied under the SEM (using backscatter imaging) and analysed using a microprobe. All Kerassia bones and teeth (in dentine and cement) showed extensive microbial focal destruction (MFD). It can be seen as zones of damaged bone, around the perimeter of the bones, around the marrow cavity and as randomly scattered foci. The MFD foci in three dimensions are ellipsoid nodules with their long axes parallel to the long axis of the bone. The rims of these nodules are permineralised. Microprobe analyses show that the apatite in the rims is enriched in calcium phosphate relative to the whole bone and calcium phosphate is depleted in the foci. The internal structure of the foci is manifest as a series of parallel microtunnels. The diameter of these microtunnels is between 150-400 nm, indicating that the invading microorganisms were bacteria. Bone material from the other Late Miocene Greek localities revealed the same or similar extensive bacterial damage. Therefore, during the Late Miocene a temperate to warm and relatively moist climate in the North-Eastern Mediterranean can be inferred.

*How to make dinosaur tracks: interpreting dinosaur footprint formation and preservation using laboratory controlled simulations

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The laboratory simulation of dinosaur footprints has the potential to yield significant information on their formation and preservation. Such studies are particularly useful as the variables involved in the trackmaking episode can be selectively investigated, with a rigorous degree of control not entirely possible in experimental animal studies. The three-dimensional study of the tracks reveals important insight into the interaction between the dinosaur foot and the substrate at the time of track formation. Vertical sections taken through simulated footprints, preserved in layered sediments, reveal a variety of both brittle and ductile deformation structures. The style and degree of this deformation is fundamentally determined by the shape of the foot, the kinematics of the trackmaker and the nature of the sediment into which the foot penetrates. The analysis of this deformation of the sediment leads to a greater understanding of dinosaur foot morphology, dinosaur gait and the environments they once lived in.

The evolutionary diversification of Palaeozoic echinoids

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Compared to their post-Palaeozoic counterparts, the palaeobiology and evolutionary history of Palaeozoic echinoids are poorly understood. In part this is due to their non-rigid tests which dissociate rapidly on death and their resultant poor fossil record. However, under favourable conditions, Palaeozoic echinoids may be preserved complete with external appendages and feeding apparatus, and where more robust Mesozoic and Cainozoic echinoid tests can be transported after death, complete specimens of Palaeozoic echinoids are found only in the environment in which they lived. This means that although there are comparatively few specimens available, the ones that do exist commonly preserve large suites of characters and provide information about palaeoenvironment. Here I present a new, cladistically derived phylogeny for the Palaeozoic echinoids and combine this with a functional morphological approach to investigate the relationship between evolutionary diversification, ecosystem utilization and palaeoenvironment of this important but poorly characterised group.

Holocene reef structure and growth at Mavra Litharia, southern coast of Gulf of Corinth, Greece: a simple reef with a complex message

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A Holocene reef at Mavra Litharia on the southern coast of the central part of the Gulf of Corinth, Greece, is constructed of a coral-algal frame, bound by laminated micritic carbonate crusts of possible microbial origin. The reef reveals a two-stage history:

a) growth of reef, without detectable ecological zonation, followed by uplift into subaerial conditions, where a cave system developed throughout the upper part of the reef. The cave system was partly filled with clastic debris washed from nearby hills of uplifted footwall blocks

b) resubmergence and colonisation of eroded surfaces by barnacles, serpulid worms and rock-boring bivalves, followed by uplift to its present setting, where much of the reef has been removed by erosion.

The relative sea-level changes represented by the history of the reef took place under a regime of presumed continuously rising global sea level in the Gulf during the Holocene; global SL rose rapidly in the early part of the Holocene up to the mid-Holocene quasi-stillstand (c.8-6.5 ka), then more gradually up to modern times. Thus the reef's history demonstrates an apparent interplay between SL rise and tectonic vertical movement against the backdrop of stepwise footwall uplift along the southern margin of the Gulf of Corinth.

The evolution of swimming among ammonoids

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Ammonoid conch geometry is the key to their mode of life, because of their poorly known soft parts. Among the conch parameters, the whorl expansion is especially significant, representing a proxy for the apertural orientation in planispiral ammonoids which grew approximately isometric. Apparently, the origin of ammonoids lies within the Bactritidae which usually had orthoconic conchs and thus downward oriented apertures. There horizontal movements were probably slow. In more derived Bactritidae with curved conchs, the aperture reached an oblique downward orientation (*Cyrtobactrites*: 20-30°). During the early Emsian, the curvature increased during phylogeny and simultaneously, the orientation of the aperture moved from oblique upward to horizontal (*Metabactrites Erbenoceras Mimosphinctes Mimagoniatites*: 40–70°). The late Emsian Latanarcestidae gave rise to four important Middle Devonian ammonoid families

(Agoniatitaceae, Anarcestaceae, Pharciceratataceae, Tornoceratataceae). Throughout phylogeny of these clades, transformations of conch geometry and orientation happened. Many apomorphic forms of these clades had similar whorl expansion rates as adults, the same almost horizontal orientation of the aperture (70-80°), smooth slender conchs, and a narrow umbilicus. These features indicate moderate to good horizontal swimming abilities, a selective advantage with respect to the search for prey, mating partners, or spawning sites.

New perspectives in palaeoscolecidans

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Palaeoscolecidans are an extinct class of vermiform organisms with a prominent annulation ranging from the Lower Cambrian to the Silurian. The outer cuticle of their segments possesses microelements mineralized by calcium phosphate. Such sclerites have been mainly isolated from carbonates. There is extensive unpublished material especially in conodont collections, at least from Laurentia. Preliminary data show a stratigraphic value of some morphotypes. Therefore, after detailed taxonomic revision, palaeoscolecidans may represent potential index fossils.

Future comparison of the microelements with larger fragments of palaeoscolecidans or whole body fossils, mainly recovered from fine-grained siliciclastics, is necessary, not least to avoid producing many parataxa. The study of material from different palaeocontinents might be of significant value for the solutions of biostratigraphical and palaeobiogeographical questions. Some taxa may be good tools to correlate from tropical realms (e.g. Laurentia) over temperate areas to cold regions such as peri-Gondwana.

Hydrothermal vent and cold seep molluscs: view from the fossil record

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Molluscs first appeared in vent and seep environments early in the Palaeozoic. A few Palaeozoic vent and seep assemblages are dominated by bivalves, but others contain no molluscs, or are outnumbered numerically by brachiopods. Some of these Palaeozoic vent and seep molluscs belong to extinct groups, common in contemporaneous non-vent and non-seep fossil assemblages. Preservation factors do not allow chemosymbiotic lifestyles to be established with any certainty for these ancient taxa. The record is better in the Mesozoic and Cenozoic, especially for seeps. Towards the later Mesozoic, brachiopods become increasingly rare in vent and seep communities, and bivalves and gastropods become the dominant shelly taxa. The Mesozoic marks the first appearance in vents and seeps of a group of chemosymbiotic bivalves (mytilids, lucinids, and solemyids) which are important constituents of modern chemosynthetic

communities, but also have Palaeozoic, non-vent, non-seep origins. The first provannid gastropods and vesicomyid bivalves appear in late Jurassic and early Cretaceous seeps, respectively. These two families are today endemic in chemosynthetic environments and have many chemosymbiotic species. Many modern vent and seep molluscs, particularly the smaller gastropods, have yet to be identified in the fossil record. In summary, Phanerozoic vent and seep deposits contain a rich and growing record of fossil molluscs. These data can be used to test phylogenetic hypotheses generated by molecular data from living chemosymbiotic molluscs.

***Application of high-resolution computed tomography in palaeontology: analysis of a Middle Devonian labyrinthodont tooth from New York State, USA**

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An unidentified labyrinthodont tooth was discovered as an isolated specimen from the Middle Devonian Panther Mountain Formation in Central New York State, USA. Studies on the internal structure of labyrinthodont teeth have traditionally relied on mechanical sectioning, resulting in at least partial destruction of the specimen. High-resolution x-ray computed tomography is a non-invasive three-dimensional imaging technique, which provides a non-destructive alternative to sectioning and serial grinding. By passing x-rays through the sample the variation of x-ray attenuation can be measured. This corresponds closely to contrasting densities within the specimen. These data are mapped as a series of two-dimensional slices, which are assembled into a three-dimensional stack with a resolution of about ten microns. The labyrinthodont tooth was scanned at the high-resolution x-ray computed tomography unit at the University of Texas, USA. Although badly degraded, marginal dentine is preserved and internal folds are present in both horizontal and vertical planes. The tooth has an open pulp cavity with the suggestion of bone extending between the folds, characters more typical of labyrinthodont tetrapod than labyrinthodont fish teeth. Further fossil discoveries from the area may help to demonstrate that this tooth represents the earliest known example of a tetrapod.

Use of Morphometrics to Identify Character States

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Much of the classic cladistic literature has opposed the idea of using morphometric methods to identify characters and their associated states. Several authors have suggested that morphometric methods are limited in this context because they produce continuous size-shape variables that must be rendered discrete by arbitrary means in order to be coded appropriately. Others have raised questions about the conformance of morphometric variables to the concept of homology. These issues may be addressed successfully in the context of a morphometric investigation by remembering that (1) the focus of any such investigation is to locate and document discontinuities in the distribution of shapes across organic forms, and (2) good systematic practice requires that variation in unified characters be considered in isolation from other such characters. If these principles are kept in mind when designing an analysis, a morphometric approach can yield substantial advantages. Moreover, use of morphometrics approaches to model the theoretical space around multivariate shape ordinations provides systematists with new tools designed to explore this space. Such explorations can improve character-state definitions as well as facilitating the discovery of new character states. These approaches are illustrated with examples drawn from invertebrate palaeontology, palaeobotany and morphological simulation studies.

The palaeoclimatic significance of the Devonian-Carboniferous boundary

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A number of Late Devonian global events have been recognised. These are characterized by significant faunal and microfloral turnover. One such event is the Hangenberg which occurs at the D-C boundary. In East Greenland the D-C boundary occurs within the 3m thick Obrutschew Bjerg Formation. This formation represents a short interval when the basin was occupied by a huge anoxic lake. During lake development the terrestrial flora initially diversifies. However the main part of the lake cycle shows the same pattern of microfloral extinctions and impoverishment as widely reported in marginal marine sediments.

There has been much recent discussion of Late Devonian glacial diamictites. We interpret these as representing episodes of glacial collapse. Such collapses occur at the climatic maximum and are accompanied by a significant strengthening of the monsoon. This caused the short-lived 'greening' of large parts of the modern Sahara Desert and the flooding event in the African lakes. The Obrutschew Bjerg Formation is seen as analogous. Clearly this interpretation relies on the precise identification of the D-C boundary in high latitude glacial diamictite bearing sections. Such sections have been investigated at outcrop in both South Africa and Bolivia.

The morphology of hyolithids and its functional implications

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Hyolithids were armoured with a four-pieced scleritome that easily fell apart after death. It consisted of a conch, an operculum and a pair of conspicuous but fragile spines called helens. While the anatomical relation between conch and operculum is straightforward, the precise position and orientation of helens has proven problematic, rendering the scleritome a puzzling "model kit". Numerous muscle scars on conch and operculum indicate that the latter provided the animal with solid surfaces for muscle attachment as well as with a protective cover. The function of helens has on the other hand remained as intriguing as their structure and form. Study of exceptionally preserved specimens has shed light on these problematic aspects of hyolithid morphology.

Helens were solid and had a shell microstructure consisting of concentric lamellae. They curved ventrally and were partially internal, extending outside the conch with the dorsal edge tilted forwards. Their internal portion did not lean against the operculum as previously believed but held free on the aperture plane. Hyolithids possessed a complex, non-seriated musculature likely involved in the articulation of the scleritome. Helens were probably mobile and could have contributed both to locomotion and stabilization.

*The influence of substrate consistency on footprint morphology: field experiments with an emu

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In order to demonstrate the influence of substrate consistency on vertebrate track morphology, field experiments were conducted by encouraging an emu to walk through prepared areas of sand and mud of different thickness and with different water content. Tracks sat in dry substrates either collapsed immediately after removal of the foot as in the case of sand, or failed to leave an impression at all as in mud. Damp sand and mud produced tracks preserving a high quality of details. With increasing water content, several variations of semi-collapsed and collapsed tracks were produced as well as related phenomena such as material ejected during withdrawal of the foot. Substrates of semi-liquid consistencies caused the track walls to flow together destroying the shape immediately after the foot was lifted. Horizontal sections through tracks sat in soft cement show that even though a track seems to have collapsed at the surface, the shape of the track is clearly recognizable at deeper levels. Lateral variation in substrate properties, such as water content, can cause tracks deriving from one individual to show highly different morphologies; this bears strong implications for the interpretation of fossil tracks and trackways.

*A Global Overview of the *lundgreni* (Wenlock, Silurian) Graptoloid Extinction Event

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The extinction event at the end of the *lundgreni* biozone was one of the most severe to affect graptoloids during the Silurian. I have assembled a database from the literature of graptoloid occurrences before and after the *lundgreni* event, recording species occurrences at the zonal level. The data were used to test the hypotheses that victims of the event were geographically restricted and that life history strategy (whether a species is K- or r-selected) determines extinction probability. Ecological theory predicts that K-selected species are less likely to survive extinction events than r-selected species. K-selected species are large, long-lived and have few offspring, most of which survive; r-selected species are small, short-lived and have many offspring, few of which survive. Geographical distribution does not appear to affect extinction likelihood. The limited data available on life history strategies indicate that K-selected species are more vulnerable to extinction than r-selected ones.

Microplankton associations and biofacies: testing Silurian palaeoenvironmental models

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Cluster and correspondence analyses of the temporal distribution of the acritarchs and prasinophyte algae through the lower part of the type Ludlow Series (Silurian) have defined recurrent associations of microplankton species and biofacies. This has enabled fine scale environmental fluctuations to be recognized. A recurrent association of endemic taxa are abundant throughout the section. These taxa are considered to be the most environmentally tolerant species. Also recognized are recurrent associations of taxa that generally coincide with the formations defined in the lower part of the Ludlow Series. Further, a recurrent association of species that are most abundant at a level where other taxa are rare suggests that some microplankton adapted to periods of environmental stress. The distribution of microplankton through the sequence support aspects of the sea level model and Jeppsson's oceanic model of environmental change.

The cranial morphology and systematics of the enigmatic basal ornithischian *Heterodontosaurus tucki* Crompton and Charig, 1962

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The discovery of a nearly complete skull of an ornithischian dinosaur exhibiting a mammal-like heterodont dentition in the Early Jurassic of South Africa was unexpected. It led to a rapid reappraisal of a number of specimens previously identified as mammal-like reptiles from similarly aged localities (*Geranosaurus* and *Lycorhinus*). Preliminary description of this skull in 1962 was not followed by a more detailed account of its anatomy. Subsequently, a well-preserved, articulated skeleton attributed to this species was recovered. The postcranial skeleton was described in 1980, but the skull remained undescribed.

The cranial anatomy of *Heterodontosaurus* is described in detail on the basis of the holotype and referred skulls. The skull exhibits an unusual degree of anatomical specialisation in such an early dinosaur; this is particularly so when compared with approximately contemporary taxa such as the basal ornithischian *Lesothosaurus* and the early armoured taxon *Scelidosaurus*. Systematic analyses that include basal ornithischian dinosaurs have adopted a fairly consistent topology with respect to the placement of *Heterodontosaurus* (and closely related heterodontosaurids) as the most basal members of the clade Ornithopoda. Study of the cranial anatomy (combined with the known postcranial material) of this taxon has provided an opportunity to reassess its systematic position within Ornithischia.

A revised high-resolution ammonite time scale for the Lower Jurassic of Great Britain

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Ammonites remain as the most important correlative tools for Jurassic marine sequences, and form the backbone of a standard Jurassic chronostratigraphic time scale, the Lower Jurassic part of this scheme being established for Britain by W.T. Dean, D.T.Donovan and M.K. Howarth in 1961. A considerable volume of work has subsequently been carried out across Europe (including in France, Germany and Britain) which has facilitated a very significant increase in resolution of this time scale through the recognition of biohorizons or horizons (= "zonules") at sub-subchronozonal level—thereby creating a high-resolution time scale with an averaged resolution of less than 120,000 years. Surprisingly, however, awareness of advances in this field seems limited in the UK, and Dean *et al.*'s now somewhat dated scheme is still widely used. The aim of this presentation, therefore, is to review the current "state of the art" for Lower Jurassic ammonite-based stratigraphy and introduce to a wider audience the potential inherent for other palaeontological and geological studies of the high-resolution time scale now available (Hettangian – 24 biohorizons in 3 chronozones; Sinemurian – 78 biohorizons in 6 chronozones; Plienbachian – 36 horizons in 5 chronozones; Toarcian – 40 biohorizons/horizons in 8 chronozones).

Phylogenetic Congruence Between Hard and Soft Part Data Sets: How Taphonomy Affects Ostracod Phylogenies

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Taphonomic bias against soft tissue preservation is widely considered to be a barrier to understanding evolutionary relationships and diversification patterns in the fossil record. A morphologically based phylogenetic analysis of a clade of lacustrine podocopid ostracods from Lakes Tanganyika and Malawi was done using hard and soft characters (PAUP, v. 4.0). Eliminating all hard part characters in subsequent analyses caused the collapse of many branches to polytomies and significantly decreased the agreement of the hard part trees. Analyses excluding all soft part characters increased the number of most parsimonious trees and decreased the resolution of the trees by creating many unresolved polytomies, but produced similar islands of stability as the original combined analysis.

This study verifies that the loss of either hard or soft part characters reduces phylogenetic resolution. It also demonstrates that more resolution was lost by omitting soft versus hard part characters, suggesting that soft part preservational bias in the ostracod fossil record may have an appreciable effect (loss of ~20%) on diversity approximations. The hard part only tree may be less resolved because those features are likely to be ecophenotypic and therefore more plastic, which is consistent with previous studies on ecologically promoted variation in ostracod carapaces.

*Halkieriids in Middle Cambrian phosphatic limestones from Australia

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Halkieriids are part of a distinctive Early Cambrian fauna preserved mostly as phosphatic and secondarily phosphatized skeletal elements. The distinctiveness of this fauna is ascribed, in part, to its preferential elimination during end-Early Cambrian mass extinction event. Newly discovered halkieriids in phosphatic limestones of the Middle Cambrian Monastery Creek Formation, Georgina Basin, Australia, now indicate that the group not only survived this extinction, but was at least locally abundant thereafter. Most of the Georgina halkieriid sclerites can be accommodated within a single species *Australohalkieria superstes* gen. et sp. nov., described and partly reconstructed here. Remaining sclerites represent two additional, rare halkieriid species. The Monastery Creek Formation provides a valuable window on Middle Cambrian life, because it provides information that is distinct from but complementary to other, similarly-aged windows, and because it represents a taphonomic window similar to those that preserve Early Cambrian small shelly problematica. A decline during the Cambrian in conditions necessary for the early diagenetic phosphatization of shallow shelf and platform limestones may have effectively closed this window, biasing apparent patterns of diversity change. Certainly, the Monastery Creek halkieriids indicate that this clade was not a short-lived biological 'experiment' but a successful and long-ranging component of Cambrian communities.

*Microfaunas across the Bathonian-Callovian boundary

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The Cornbrash Formation (Upper Bathonian-Lower Callovian, Middle Jurassic) forms a thin, persistent outcrop from the Yorkshire coast to Dorset. Its abundant and well-preserved macrofauna, especially the Brachiopoda and Bivalvia, have been well documented since the 19th century. A faunal turnover has been reported at the boundary between the Lower and Upper Cornbrash (Bathonian-Callovian boundary) and it is here that Raup and Sepkoski (1984, 1986) placed one of the missing peaks in their periodic extinction theory. However, on closer examination, few brachiopod or bivalve species actually become extinct at this horizon, merely diminish in abundance.

An independent test of the hypothesis is offered by the microfauna of the Cornbrash Formation, which is more poorly known. Foraminifera genera present include *Citharina*, *Dentalina*, *Frondicularia*, *Lenticulina* and *Haplophragmoides*; as with the macrofauna, specimens are abundant and generally well-preserved. Basov and Kuznetsova (2000) recorded the highest foraminiferal extinction rates in the Jurassic at the Bathonian-Callovian boundary. However, the NW European record suggests that there is no obvious change in the microfauna at the boundary that cannot be explained by local and mesoscale parameters.

Body building in *Halkieria* and comparisons with chitons and other possible stem-group molluscs

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Models of articulated skeletons (scleritomes) of *Halkieria evangelista* Conway Morris & Peel from the Cambrian of Greenland are used to reconstruct the growth of halkieriids. As in chitons (polyplacophorans), growth occurred inboard from the edge of the body along narrow zones that connect the lateral growing edges of the anterior and posterior shells. Also, new rows of cultrate sclerites were added near the body margins as growth proceeded. These similarities with polyplacophorans are reinforced by the presence of relict sclerites within the shell plates (valves) of the Cambrian chiton *Matthevia*. *Matthevia* valves resemble the fused-sclerite shells of the Early Cambrian fossil *Maikhanella* (Bengtson, *Lethaia* **25**, 401, 1992) and may also serve as morphological intermediates between the tissue-filled sclerites of the halkieriids and sensory esthetes embedded in the outer layer of the valves of living chitons.

If this assessment of the growth of *Halkieria evangelista* is correct, its affinities lie closer to the Mollusca than to the Annelida or Brachiopoda (Conway Morris and Peel, *Phil. Trans.* **B 347**, 305, 1995). However, exclusion of halkieriids from the molluscan crown group (all descendants of the last common ancestor of living molluscs) depends upon the placement of the class Aplacophora. If aplacophorans are secondarily simplified, perhaps by progenesis (Scheltema, *Biol. Bull.* **184**, 57, 1993), halkieriids may belong to the molluscan stem group. Alternatively, if aplacophorans

are primitively vermiform and spiculose, halkieriids may be members of the molluscan crown group. In any case, other mollusc-like organisms such as hyoliths may be used to explore features of early development in stem group molluscs. Pooling all information from living and extinct taxa provides a paradigm for body building in primitive lophotrochozoans.

Constructional Morphology of Pelagic Crinoids

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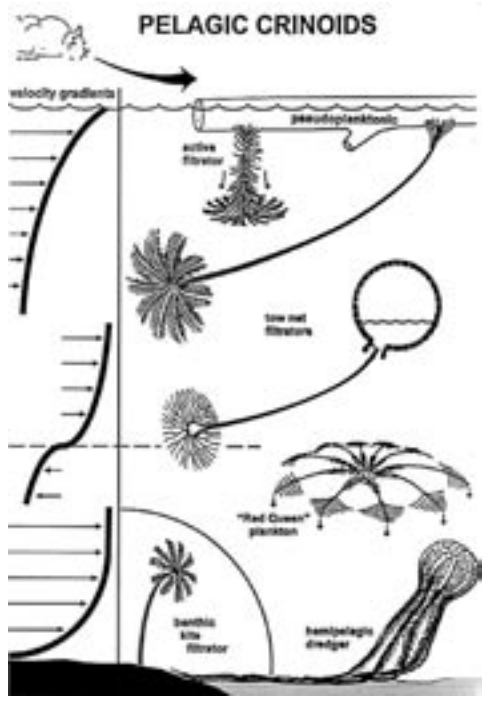

While all modern crinoids are benthic filter feeders, some fossil forms from low-oxygen Lagerstaetten were probably pelagic. Most pseudoplanktonic forms were attached to driftwood (*Seirocrinus*; *Traumatocrinus*); they had long fast-growing, rope-like stems and enlarged, permanently splayed filter fans, as required by a tow-net function. The short and heavily cirrated stem of *Pentacrinus briareus*, however, suggest active filtration. If the buoyant lobolith acted as a swim bladder, *Scyphocrinites* could use its tow-net in the velocity gradient near a boundary layer. Paradigms are different for stemless forms, whether they floated passively over the bottom (*Uintacrinus*) or filtrated actively in the water column (Roveacrinids and *Saccocoma*). Our theoretical models characterize peaks in the adaptive landscape and can be checked against taphonomic, morphological, and evolutionary evidence.

Ancient weavers on the silk road: Jurassic spiders from China

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Among the feathered dinosaurs, salamanders and abundant insects, a collection of more than 60 new specimens of spiders from the Upper Jurassic Yixian Formation and the Middle

Jurassic Jiulongshan Formation of north-east China has been amassed and is described briefly here. Until now, only two spiders were known from the Jurassic period worldwide; thus the new collection represents an enormous addition in the fossil record of these rarely preserved animals. The spiders are preserved in lacustrine deposits, and were apparently knocked into the water by volcanic ash falls. Their preservation is exquisite, allowing fine morphological details to be observed. Many of the new specimens belong to the extant orb-weaver family Uloboridae and superfamily Araneoidea. These are already known from the Mesozoic. There are also rare members of the ground-dwelling fauna. Because of the rarity of Mesozoic spiders, the new finds shed no light on stratigraphic problems of the Jehol biota.

Palaeobiology of Carboniferous microcrinoids

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Most Carboniferous microcrinoids (crinoids with adult thecae less than 2mm high) belong either to the disparid family Allagecrinidae or to the cladid family Codiacrinidae. They inhabited environments ranging from relatively deep, low energy basin floor, through higher energy, open shelf, to shallow water, inner shelf. Allagecrinid crowns were probably raised higher above the substrate than those of codiacrinids of comparable thecal size; the theca of one codiacrinid was cemented directly to the substrate. Allagecrinids were suspension feeders that used the arms to capture minute particles that entered the theca through slits between the opened orals. Many codiacrinids were either armless or had less than five arms. They probably fed using podia that were exposed when the orals were pushed open. Both types of microcrinoids may also have utilised dissolved organic matter as a nutrient source. There is tenuous evidence that allagecrinids had a single internal gonad. The small node on the CD oral was a hydropore not a gonopore: gametes were shed by opening of the orals. Larvae of such small crinoids might have been expected to be planktotrophic but the presence of brooding structures in one allagecrinid suggests that some, at least, were lecithotrophic.

***Microevolution of the charophyte genus *Harrisichara* across the Eocene-Oligocene transition in the Isle of Wight, Southern England**

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The Eocene-Oligocene transitional strata in the Isle of Wight offer a unique opportunity to study how the terrestrial realm responded to the global cooling event that occurred at this time. Three diverse biotic elements [charophyte gyrogonites, *Stratiotes* seeds and rodent teeth] are being investigated for microevolutionary change. Results will be used to assess how terrestrial biotas responded to Eocene-Oligocene cooling and to attempt to erect an integrated biostratigraphic framework. Charophytes are currently used in the European correlation charts

for the Palaeogene and therefore have a known biostratigraphic value in correlating across the terrestrial basins of Northern Europe. Studies currently being carried out (using image analysis and morphometrics) aim to show how microevolutionary change can be used to refine the biozonation and increase resolution of the zones.

Microevolutionary results will be presented from a study of *Harrisichara* through a number of levels within the Solent Group in Southern England. Up to 150 specimens from each level have been picked and various measurements made using image analysis software. Principle component analyses have been carried out using six defined independent variables including eigenshape values, length/width ratio and intertubercle ornament density.

***The Early Cambrian *Mickwitzia* from Greenland and Nevada and the origin of the brachiopods**

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The affinities of the Early Cambrian bivalve *Mickwitzia* Schmidt, 1888 have been discussed for more than a century. Conventionally included in the paterinid brachiopods, it has alternatively been excluded from the phylum Brachiopoda or placed in its stem-group. Etched material of *M.* cf. *occidens* Walcott, 1908 from the Early Cambrian of Greenland and Nevada demonstrates that *Mickwitzia* shares a number of characters with linguliform brachiopods: a lingulid-like juvenile shell with trails of nick-points reflecting the movement of marginal setae; a lingulid-like pseudointerarea with a pedicle groove in juvenile and early mature ventral valves; an organophosphatic shell with a columnar lamination homologous with that characterizing acrotretides. The shell, however, is also pervaded by striated apatitic tubes indistinguishable from those permeating the sclerites of the problematic *Micrina* Laurie, 1986. The tubes are presumed to have contained setae and are absent in all crown group brachiopods. These features suggests that *Mickwitzia* is a stem group brachiopod.

Origins of teeth amongst jawed stem group gnathostomes

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Placoderms as the sister group of crown group gnathostomes represent the most primitive forms with jaws, but the consensus view is that teeth, homologous with those of chondrichthyans, acanthodians and osteichthyans, are absent. Lack of structural evidence for both regular dentine and patterned successional teeth in placoderms is the basis for this opinion. Thus the co-evolution of teeth with jaws and their origin is questioned and instead teeth, those developed from tooth specific tissues (dental lamina) are proposed as a synapomorphy of all except placoderms.

Placoderms have statodont dentitions, those not replaced but adapted to wear by hard tissue growth. However, amongst arthrodires, alongside worn cutting edges there are ordered rows of new conical structures providing dental tissues during growth. Sectioned cones show regular dentine, formed around a pulp chamber, and a tissue different from semidentine of the dermal tubercles. Together with sequential unitary addition, comparable with tooth addition in gnathostome jaws, these demonstrate teeth in derived placoderms. The origin of teeth late in placoderm phylogeny suggests that this evolution occurred independently at least twice within jawed gnathostomes. These observations challenge the consensus view of the origins of teeth and propose the presence of a dental lamina in certain placoderms.

Composition, depositional setting and palaeoecology of Siphonodendron biostromes in the late Viséan of SE Ireland

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Siphonodendron biostromes are recorded from well-bedded dark grey limestones of Brigantian (late Viséan) age in counties Carlow and Kilkenny (SE Ireland). They occur in the Clogrenan Formation, which is exposed in several working quarries within the region. The limestones form part of a widespread shallow water shelf sequence in which periodic subaerial exposure is recognised by palaeokarsts and palaeosols. Two coral biostromes in the middle of the formation can be correlated between quarries 5 km apart and a third biostrome is developed higher in the formation. All of the biostromes are dominated by *Siphonodendron* colonies and are usually tabular with pronounced peripheral growth strategies. The dimensions of fasciculate colonies are typically 15-20 cm high and 50-90 cm in width, but some colonies can reach 4.5 m in width. The corallites in many colonies have the same upper growth level. Associated rugose corals in the biostromes are *Diphyphyllum*, *Lonsdaleia* and the cerioids *Lithostrotion* and *Actinocyathus*, together with the tabulate *Syringopora*, but all form accessory roles in constructions. The youngest biostrome is the most diverse with 13 genera and 15 species. Gigantoproductid brachiopods are an important related element, commonly forming concentrations of *in situ* shells below or above the *Siphonodendron* colonies. Comparisons are made with other upper Viséan *Siphonodendron* biostromes in NW Ireland, northern England and SW Spain.

***Waptia fieldensis*, a possible crustacean from the Middle Cambrian Burgess Shale of British Columbia, Canada**

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Examination of approximately 1,300 specimens of *Waptia fieldensis* has led to an improved understanding of the biology of this animal. *W. fieldensis* possesses a bivalved carapace that

covers the cephalon and most of the thorax. The cephalon possesses up to five segments plus a complex array of feeding appendages, made up of three to five limbs. One pair of elongate antennae is present, as are a pair of short lobed structures positionally equivalent to the second antennae of Crustacea. The anterior thorax possesses four somites and has segmented, stenopodous-like limbs, while the posterior thorax demonstrates six gill-like limbs. The abdomen is limbless and is made up of five segments plus a telson and bilobed tailfan.

The somite and limb patterns demonstrated by *W. fieldensis* closely resemble those of many modern Eumalacostracan groups, suggesting Walcott's original placement of *Waptia* within the Crustacea may have been correct. The presence of what may be second antennae further supports a crustacean relationship for *Waptia*. The recent description of *Ercaia miniscula*, a crustacean from the Early Cambrian Chengjiang biota of China, further supports the notion that Crustacea may also have existed in the Middle Cambrian Burgess Shale.

***Trackways meet trackmakers: the composition of early tetrapod communities**

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A Late Carboniferous (Westphalian D; Moscovian) footprint fauna from Alveley, southern Shropshire, UK, is a significant example of an early, marginal-terrestrial tetrapod community. As the only vertebrate ichno-assemblage of its age in Europe, it presents a valuable insight into the interval between the appearance of tetrapods in the Devonian and the amniote dominated faunas of the Early Permian. Ichnodiversity has been determined with the aid of numerical, multivariate methods, and morphological variation within the assemblage has been studied, providing a comprehensive review of the ichnofauna. However, in order to produce a full palaeoecological interpretation, enabling comparison with skeletal assemblages, an accurate method of determining trackmaker identity using selected trackway features is required. Synapomorphy-based character analysis has been combined with phenetic and coincidence correlation techniques to examine trackmaker identities in detail. This is the first such study that has been undertaken on Late Palaeozoic ichnofaunas, ultimately aiming to chart the evolution of terrestrial tetrapod communities through the Late Carboniferous and Early Permian.

Significance of a recently discovered, exceptionally diverse, Early Triassic marine assemblage from Oman

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An exceptionally diverse Early Triassic fauna has been discovered in the Wadi Wasit region of the Central Oman mountains. The fauna is Griesbachian in age (on the basis of abundant conodonts and ammonoids), and was deposited in a well-oxygenated, storm-winnowed seamount off the Arabian platform margin. The earliest Griesbachian assemblage (*parvus* Zone) is a low diversity, opportunistic fauna dominated by the bivalves *Promyalina* and *Claraia* (typical of the aftermath

of the end-Permian extinction event). The mid-upper Griesbachian sediments (*isarcica* and *carinata* Zones) contain an incredibly diverse and partially silicified benthic fauna of bivalves (dominated by large *Claraia*), ten gastropod taxa (including large *Naticopsis*), the articulate brachiopod *Crurithyris*, a new and locally abundant rhynchonellid, a new, undescribed crinoid, fragmentary echinoids and ostracods. This fauna is more diverse and ecologically complex than "typical" mid-late Griesbachian age faunas, described from oxygen-restricted settings worldwide. This supports the hypothesis that the apparent delay in recovery after the end-Permian extinction can be attributed to widespread and prolonged benthic oxygen restriction. However, if the anoxic event also caused the extinction, then Permian holdovers would be expected in this fauna. None are found, casting serious doubts on the hypothesis that oceanic anoxia was an important kill mechanism.

Cambrian food chains: new perspectives

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Fossil evidence from exceptional biotas attests to the existence of diverse marine ecosystems in the Cambrian, but still very little is known of their functioning (e.g. primary production, food sources, feeding strategies, prey/predator relationships). A set of new information obtained from the Maotianshan Shale (Early Cambrian) and the Kaili (early Middle Cambrian) Lagerstätten from South China offers new perspectives for the reconstruction of Cambrian food chains. This includes:

- Arthropod gut contents with identifiable skeletal remains (eodiscoid and possibly bradoriid arthropods)
- Preserved digestive systems and feeding organs
- Possible coproliths and isolated gut contents with recognisable elements such as carapaces of bivalved arthropods (e.g. bradoriids, waptiids), hyolith shells and fragments of trilobite exoskeletons

In the Early Cambrian, predators were present in endobenthic (e.g. priapulid worms), epibenthic (several arthropod groups) and midwater niches (e.g. anomalocaridids, medusoid-like eldoniids, ctenophores). Prolific organisms living at the interface layer between water and sediment (e.g. vagile bradoriid arthropods and larvae; poorly motile epibenthic hyoliths) and in the lower part of the water column (e.g; demersal phyllocarid-like arthropods such as waptiids) most probably constituted the major food source for the macrophageous predators.

*Calcareous nannofossil assemblages during the Messinian Salinity Crisis: evidence from the Polemi Basin, Cyprus

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Nannofossil assemblages within the Messinian units from the Polemi Basin, Cyprus, provide a unique picture of environmental changes associated with the Messinian Salinity Crisis. Results indicated that the intercalated marls, chalks and clays between the Messinian gypsum units were autochthonous and deposited in a marine environment. The large variations were found in nannofossil assemblages, suggesting a highly fluctuating environment. *Reticulofenestra minuta*, *Dictyococcites antarcticus*, *Helicosphaera carteri* and *Umbilicosphaera jafari* are suggested to be r-mode opportunists, adapted to a eutrophic, unstable environment and capable of establishing massive blooms; *Sphenolithus abies* occupied more stable environments. *R. minuta* is indicated to be able to tolerate variations in salinity. Fluctuations in nutrient levels have been interpreted to be the primary factor controlling the alterations in nannofossil assemblages. The calcareous nannoplankton results were integrated with those of the siliceous diatoms and used to formulate a model of the palaeoenvironment, indicating that the Polemi Basin was a semi-enclosed, neritic to littoral environment, subject to repeated influxes of marine and fresh water.

Early ontogenetic development of blastoids

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Postembryonic ontogeny of blastoids follows a multistage developmental path similar to modern comatulid crinoids, such as *Antedon*. In *Antedon*, the prejuvenile stage lasts about four months, and includes: 1) the doliolarial stage, which lasts two to three days; 2) the cystidian stage, which lasts about a week; and 3) the pentacrinoid stage, which lasts about fifteen weeks. Specimens that would be classified as the cystidian stage in the comatulid life cycle were the subject of pioneering studies of the early ontogeny of blastoids. In addition, *Passalocrinus*, originally described as a microcrinoid, has been determined to be a juvenile blastoid. The presence of oral plates places *Passalocrinus* in the cystidian stage of development. It has been hypothesized that *Passalocrinus* developed into typical adult blastoid morphology by resorption of the oral plates and development of ambulacral tracts and lancets. Specimens of juvenile blastoids from Lower Carboniferous black shales from Xinxu, Guangxi Province, Peoples Republic of China demonstrate an intermediate stage between the cystidian stage (*Passalocrinus*) and adult blastoid morphology. Basal and radial plates are well developed, although deltoids and orals are lacking. Initial basal and radial plates are characterized by microperforate stereom and are surrounded by 44 to 50 distinct growth lines. The oral surface lacks well-developed ambulacra,

but has food grooves in each ray leading to three sets of terminal brachiolar(?) attachment pits. Based on this material, we conclude that blastoids had multi-staged ontogenetic development similar to that seen in modern comatulid crinoids.

Tantalizing fragments of the earliest land plants

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There is a huge disparity between the first appearance of microfossil and megafossil evidence for the earliest land plants. The earliest evidence for land plants is dispersed spores that first appear in the Llanvirn (Mid Ordovician). It is not until the Wenlock (Late Silurian), some 40 million years later, that the earliest undisputed land plant megafossils occur. It is generally considered that the early spore producers were non-vascular land plants (bryophytes). These almost certainly lacked recalcitrant parts and thus had very low fossilization potential (spores excepted). It is not until much later that vascular plants (tracheophytes) evolved. These probably possessed recalcitrant (e.g. lignified) parts and thus had much greater fossilization potential. The first appearance of early land plant megafossils possibly coincides with the appearance of tracheophytes. Because of the absence of megafossils, little is known of the earliest bryophytic land plants. Recently, however, top sieving during routine palynological processing of Caradoc (Ordovician) deposits from Oman has produced relatively large fragments of these plants. These consist of spore masses and fragments of sporangia. These fossils confirm that the early dispersed spore record does indeed represent the earliest land plants, and provide the first tantalizing evidence for the nature of the producers.

*Conodonts, cladistics and the fossil record

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Most phylogenetic hypotheses of conodonts have been reconstructed on the basis of the stratigraphic distribution of taxa. Cladistic analysis, based on morphological data alone, includes no *a priori* assumptions about stratigraphic ordering. The resulting phylogeny can therefore be utilized in further applications based on evolutionary data, such as assessment of the fossil record and biogeography.

The conodont fossil record putatively represents one of the best archives of an extinct lineage. It has been appreciated for its richness and is widely used in local and global biozonation schemes throughout the Palaeozoic and Triassic. Despite the extensive use of the conodont fossil record in biostratigraphy, its quality has never been critically assessed. In this study, the fossil record of the Silurian conodont genus *Kockelella* has been investigated. Two independent methodologies have been used, the fit of a cladistic hypothesis to stratigraphic data and the calculation of confidence intervals. Both approaches indicate incompleteness in the fossil record of conodonts.

The resulting phylogeny of *Kockelella* has also provided the basis for a study in which palaeobiogeography and phylogeny have been combined. The results constitute a powerful tool in the understanding of evolutionary patterns and processes within the genus.

The end-Permian mass extinction: sudden or gradual?

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The speed with which the late Permian mass extinction happened has long been a subject of debate. Nearly 50 years ago Schindewolf challenged the prevailing consensus of a protracted extinction spread over many million years. Using evidence from the Salt Range of Pakistan he suggested that the extinction was instantaneous and may have been caused by a supernova. Perhaps because of his non-trendy, extra-terrestrial extinction mechanism, Schindewolf's ideas gained few adherents at the time. However, over the past few years "Schindewolfian rapidity"—to coin a phrase—has begun to gain respectability. Based on detailed studies of marine boundary sections, particularly those at Meishan in China and the Dolomites of Italy, several workers propose that the end-Permian mass extinction was very rapid and perhaps even instantaneous. However, distinguishing between a rapid and an instantaneous extinction event is not easy and neither the Chinese nor the Italian sections are ideal for resolving this problem. The Meishan section is ultra-condensed (sedimentation rates < 1 m/myr) and in the Dolomite sections the extinction level corresponds to a change to dolomitised, peritidal oolites—hardly ideal facies to determine last appearance data. The global synchroneity of the end-Permian extinction has also yet to be fully determined, but recent work on boundary sections in southern Tibet suggest a considerable diachroneity. This region lay at high southern palaeolatitudes and it records a considerably delayed extinction crisis, perhaps as much as one million years after the crisis occurred in lower palaeolatitudes. Therefore instantaneous kill mechanisms are not applicable to this particular mass extinction.

Calamari catastrophe

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A new exposure in the Oxford Clay Formation of southern England, equivalent to the famous and now inaccessible lagerstätte at Christian Malford, Wiltshire, has yielded numerous coleoid cephalopods with phosphatized soft-tissues. Most of the coleoids from the new locality, and some from the old one, are preserved in closely associated "pairs." Individuals within each "pair" are mutually aligned and may be either of a single species and of a similar size, or of two different species. It is proposed that the coleoids formed large schools that were killed *en masse*, together with other elements of the associated fauna, in one or more catastrophic mass mortality events that affected a significant area. During the event(s), many coleoids preyed upon

moribund fish and other coleoids before becoming overcome themselves. Phosphatization of their soft-tissues was facilitated by the large number of associated decaying carcasses which had the effect of augmented levels of dissolved phosphorus in the sediment.

Walking with Millipedes: Kinematics of Locomotion in *Polyxenus* and Implications for Reconstructing the Functional Morphology of the Palaeozoic Millipede *Arthropleura*

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The kinematics of walking in the penicillate millipede *Polyxenus anacapensis* were analyzed using high speed video and digitization software and compared to that of representative chilognath millipedes. The parameters measured included speed, stepping frequency, stride length, angle of appendage swing, period, ratio of protraction to retraction, and phase lag. When *Polyxenus* locomotes at relatively low speeds contralateral legs step synchronously and footfalls plot in a continuous series. In contrast, when *Polyxenus* locomotes at relatively high speeds contralateral legs step alternately and footfalls plot in discrete clusters. This difference in trackway morphology is due largely to an increase in stride length generated through a stretching of the body at faster speeds. Chilognath millipedes locomote with contralateral legs stepping synchronously at all speeds and their skeletomuscular anatomy does not allow for significant elongation of the trunk. The trunk ring architecture is similar in Polyxenida and the extinct giant Palaeozoic millipede *Arthropleura*. Large *Diplichnites* trace fossils attributable to *Arthropleura* are well known from North America and Europe. *Arthropleura* produced two distinct types of trackways: those consisting of a continuous series of footfalls and those with footfalls grouped into crescentic clusters. Given the morphological similarities between *Polyxenus* and *Arthropleura*, it seems reasonable to hypothesize that *Arthropleura* also utilized distinct gaits at different speeds.

The origin of metazoan reefs: Neoproterzoic of the Nama Group, Namibia

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Skeletal metazoans are first found within long-established microbial reef communities in the late Neoproterozoic, coincident with the Ediacara biota (~550 Myr BP). This fauna includes large, modular, metazoans with biologically controlled biomineralization, appearing some 15 million years earlier than previously documented. This begs the questions, were any innovations necessary for metazoans to become part of reef communities? And what were the origins of their various ecological roles?

Three genera of reef-associated metazoans are now known from the Nama Group of northern Namibia, Cloudina, Namacalathus and Namapoikia. All showed gregarious behaviour, but occupied notably different ecological niches within thrombolite-stromatolite-dominated reefs. The problematicum Cloudina appears to have been a generalist, occupying soft-sediment as well as hard-substrate reef settings, whereas the similarly problematic *Namacalathus* had a specialist stalk-like holdfast structure. Both these genera were solitary and weakly biomineralised. By contrast, modular *Namapoikia,* which reached up to 1m in diameter, had the ability to encrust, and has been found in a notably unusual niche: attached to the vertical walls of synsedimentary reef fissure systems. *Namapoikia* shows a complex and robust skeleton, and probably represents a cnidarian or poriferan. These few occurrences suggest that both generalists and specialists were present within the earliest metazoan communities, but that they occupied a diverse range of ecological niches.

Reserve: *Solenopora* is not an alga

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For over one hundred years the Ordovician fossil *Solenopora* Dybowski has been widely considered to be a calcified red alga. The type species, *Solenopora spongioides*, consists of tubes with longitudinally flexuous walls, lobate-petaloid cross-sections 30-175 μm across with septal projections, and only sporadic cross-partitions. This internal micromorphology is not characteristic of calcified red algae, but is consistent with the original interpretation of *Solenopora* as a chaetetid, and with subsequent recognition of chaetetids as sponges. *Solenopora* is widely misidentified in Silurian and younger rocks. Removal of *Solenopora* from the algae underscores the need comprehensively to reassess the palaeoecological and phylogenetic significance of numerous disparate Ordovician-Miocene fossils currently classed as solenoporaceans.

Poster presentations

Poster presentations will be in the Department practical labs on the second floor, in conjunction with morning coffee (10:30–11:00), lunch (1:00–2:00) and afternoon tea (3:30–4:00); they will be attended during the morning coffee break and lunch. Half of the posters will be presented on each day, arranged alphabetically according to author: Anenome to Märss/Miller on Monday, Moore to Zuykov/Fritsch on Tuesday.

Abstracts for poster presentations

Paleocene and Eocene mammal bearing deposits from the Great Divide Basin, Southwestern Wyoming

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The Great Divide Basin is an internal drainage basin surrounded by two diverging branches of the Continental Divide in Sweetwater County, Wyoming, USA. It forms the eastern part of the Greater Green River Basin, an area of extensive deposition of early Tertiary sediments that has yielded some of the best known mammalian faunas from the early Eocene of the American West. Following preliminary investigations by USGS and Smithsonian Institution field parties in the late 1950s and early 1960s, we began systematic investigations into the palaeontological resources of the Great Divide Basin in 1994.

Eight field seasons of palaeontological and geological investigations in early Tertiary sediments of the Great Divide Basin have yielded approximately 7,000 catalogued mammalian specimens from more than 50 localities spanning the Palaeocene-Eocene boundary. This time interval includes the latest Palaeocene thermal maximum (LPTM), a period of rapid global warming coinciding with the first appearances of many mammalian taxa in North America, Europe, and Asia. In this poster, I review the fauna from several different sets of localities ranging in time from the middle Clarkforkian to the late Wasatchian. Special attention is paid to the biostratigraphic and stratigraphic relationships of these localities and their faunas.

Yochelcionellids from Northern Greenland

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Yochelcionella are small cap-shaped molluscs, of Cambrian age, easily identifiable by a prominent snorkel on the sub-apical wall. Globally, twenty-three species, including seven in open nomenclature, have been reported. To this four new species are added from the Lower Cambrian of Peary Land North Greenland: *Y. greenlandica* sp. n., and *Y. americana* Runnegar and Pojeta, 1980, from the Aftenstjerneso Formation, *Y. paralleldalensis* sp. n., from the Paralleldal and Henson Gletscher Formations from the Brfnlund Fjord Group, *Y. gracilis* sp. n., and *Y.* sp. n.. The palaeogeographical range of *Y. americana* is extended. Palaeogeographic maps are included to illustrate the dispersal of species during the Cambrian.

The ichnofossil record across the Triassic/Jurassic Boundary

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The effects of the end Triassic mass extinction on the marine trace fossil record has been examined in England and Austria. Locally in England, there is heavy bioturbation immediately prior to the Late Rhaetian extinction horizon, with *Diplocraterion*, *Arenicolites*, and *Rhizocorallium* recorded. There is a short interval of unbioturbated sediments above the extinction horizon, with thoroughly bioturbated sediments reappearing before the boundary between the Rhaetian and the *planorbis* zone of the lower Hettangian. However, the ichnotaxon *Rhizocorallium* does not re-appear until the upper *planorbis* zone, while *Diplocraterion* and *Arenicolites* do not re-appear until the upper *angulata* zone. *Diplocraterion*, on its re-appearance, is significantly smaller than its pre-event counterparts.

The Rhaetian sediments of Austria are thoroughly bioturbated where examined some 60 metres below the Rhaetian/Hettangian boundary, with *Rhizocorallium*, *Diplocraterion*, and *Zoophycos* recorded. Immediately below the boundary itself, however, these ichnotaxa are absent. Above the boundary, laminated sediments are common throughout the Hettangian, and the ichnotaxa found in the Rhaetian are not recorded in either the Hettangian or early Sinemurian. The extinction event in Austria thus apparently began at an earlier stage than in England, and the recovery interval of the pre-event fauna is evidently longer.

The Paleo/Mesoproterozoic Stirling Biota

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The Stirling Biota in Western Australia is between 2.0 and 1.2 Ga old and is represented by trace fossils and discoidal fossils in low-grade metamorphic sandstones. The discoidal fossils have previously been interpreted as Ediacaran, but are of uncertain nature. The associated trace fossils nevertheless indicate the presence of animal-like organisms. The traces are preserved in convex hyporelief on the sole of a thick bed of fine-grained sandstone. They consist of fine ridges, about 0.5–1.0 mm wide and high, forming parallel-sided pairs, 1.5–2.5 mm wide and

posters

up to more than 2 cm long. The ridge-pairs may be straight, but usually curve more or less irregularly. A recurring morphology is characterized by the ridges at one end coming together in a U-shape and at the other end flaring to about 3.5 mm width before terminating. There is no evidence of deeper penetration into the underlying sediment. The ridges are interpreted as natural moulds of mucus-reinforced sediment strings formed by the surface movements of a vermiform organism. The organism had well-developed mucus-producing capacity and probably a hydrostatic skeleton to allow it to change shape. Whereas in today's biota this would be a description of an animal, it is possible that the traces were made by extinct multicellular or syncytial organisms outside the crown-group metazoans. Whichever type of organism made the traces, the Stirling biota offers a glimpse of a Mesoproterozoic or even Palaeoproterozoic biosphere which was more complex than the singularly microbial–algal world that is usually assumed.

Two exceptionally-preserved Ordovician sponge faunas from Mid Wales

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The Palaeozoic sponges of Avalonia have been barely studied for over a century, and it is normally assumed that fossils are so rare and non-diverse as to be of little importance. This poster introduces two Middle Ordovician faunas from disparate palaeoenvironments of central Wales, that contradict this view. The Llandegley Rocks site (middle Llanvirn: *murchisoni* Biozone) contains at least 15 species of spicular and aspicular demosponges, hexactinellids and a heteractinid from very shallow, coarse siliciclastics, preserved as silicified external moulds. In two specimens, silicification was sufficiently rapid to preserve parts of the proteinaceous skeleton. A root-tuft like sponge, *Pyritonema*, dominates the fauna, but is shown to be a monaxonid hexactinellid derived from lyssakids. The Llanfawr Quarries locality (basal Caradoc: *gracilis* Biozone) preserves about 15 species (dominantly reticulosid hexactinellids, and a hazeliid demosponge) in black mudstones. The fauna occurs at several horizons, representing different communities, and includes *Asthenospongia* Rigby, King and Gunther, and a strongly spinose relative, a species of *Cyathophycus,* a variety of early reticulosans including some with dermal specialisation, and two new demosponges.

A new stem tetrapod from the mid-Carboniferous of Northern Ireland

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We report on the first Carboniferous tetrapod specimen discovered in Northern Ireland, and one of the most primitive tetrapods known from the UK. The specimen consists of a partial left jaw ramus showing sufficient features to diagnose it as a new taxon. The specimen was discovered

in 1843 by Portlock, described as a rhizodont fish and housed with the British Geological Survey. However, this specimen belongs to an undoubted early tetrapod. The precise locality is uncertain, but it derives from near Londonderry, possibly Maghera. Palynological evidence is equivocal, ranging from late Viséan through early Westphalian, but samples of other specimens from Maghera are Tournaisian (CM zone), which would make it one of the earliest tetrapods known. The specimen extends the geographical range of known Early Carboniferous tetrapods, which have now been found much further westwards in the British Isles than previously reported, and suggests the possibility of further discoveries in this region.

A preliminary analysis of lower jaw characters places the new taxon in the neighbourhood of "cf.*Tulerpeton*" (late Famennian jaw material from Andreyevka, Russia) and *Whatcheeria*, above all other Devonian tetrapods, and below *Crassigyrinus*, *Greererpeton*, *Megalocephalus* and an anthracosaur-temnospondyl clade. It may belong to an early and wide-ranging post-Devonian tetrapod radiation.

Tracking Dinosaurs in Scotland

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The first *in situ* dinosaurs from Scotland were discovered at the top of the Duntulum Formation (Bathonian, Jurassic) near to Staffin in northeastern Skye at the beginning of this year. Fifteen individual tridactyl footprints were recorded of which two pairs appear to be partial trackways. The footprints are preserved as natural casts on a mud-cracked calcareous sandstone surface. The individual track sizes range from about 30cm to over 50cm in length with narrow to broad digits suggestive of having been made by a medium to large bipedal dinosaur. These are also the youngest record of dinosaurs in Scotland and the largest!

Middle Cambrian cambroclavids from the Cantabrian Mountains (northern Spain): new clues for systematic re-appraisals

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Recent etching of glauconitic bioclastic limestones (Beleño facies) from the first Middle Cambrian biozone (*Acadoparadoxides mureroensis*) of the Láncara Formation (Esla nappe, Cantabrian Mountains) has yielded key cambroclavids to test the phylogenetic relationships of these sclerites, commonly reported from the Lower Cambrian. Two species are distinguished: *Parazhijinites guizhovensis* and *Wushichites* n.sp. Although Bengston *et al.* (1990) reported the genus *Wushichites* as a junior synonym of *Cambroclavus*, and Conway Morris *et al.* (1997) considered *W. polyedrus* as a junior synonym of *W. minutus* (the type species), the new Cantabrian species (the first finding of this taxon outside China) allows us to re-erect formally the genus, in which a second species is now recognized.

posters

A new approach to interpreting palynological data from the Late Carboniferous tropical coal forests

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Using the dispersed palynology of the Late Carboniferous (Pennsylvanian) tropical coal forests for vegetational analysis has traditionally been difficult because we did not know which plants produced many types of pollen and spore. A.H.V. Smith identified distinctive palynological associations at different levels within coal seams, but it was difficult to relate this to vegetation change in any detail. However, this situation has changed through recent studies on *in situ* spores and pollen, and we can now start reinterpreting the dispersed palynological data. Evidence from South Wales, the Forest of Dean, the Dobrudzha Coalfield (Bulgaria) and the Sydney Coalfield (Cape Breton) suggests a progressive expansion of the lycophyte-dominated wetlands during the late Westphalian D, resulting in a distinct *Lycospora*-spike at the Westphalian-Stephanian boundary. Traditionally, work on the dispersed palynology of these deposits has been mainly on the coals, but our evidence suggests that the palynology of the clastic deposits gives the best evidence for the overall composition of the forests.

Questioning the tetrapod diversity of a Jurassic island, Glamorganshire

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Non-mammalian tetrapod remains from a new Early Jurassic fissure fill in Pant quarry, South Wales, indicate a more diverse fauna than previously described. A small region of Glamorgan, named St. Brides Island, remained above water throughout Hettangian times, before being submerged early in the Sinemurian. The average St. Brides *Hirmeriella* faunal associations, named after the widespread conifer fossil *Hirmeriella muensteri*, consists of only three tetrapod genera, whereas the new Pant 4 fissure has revealed many more. In addition to the usual one lepidosaur (*Gephyrosaurus bridensis*) and two mammalian genera (*Morganucodon* and *Kuehneotherium*), remains of sphenodontians, tritylodontids, archosaurs, and other mammals have been discovered. Concentrating on non-mammalian components (Pam Gill, another Bristol postgraduate, is examining the mammalian finds), the previous identification of three new sphenodontid and up to three new tritylodont species from the fissure is analysed. Material from the new fissure, excavated in 1973 and 1978, is described. Dating of the fauna is complicated by the depositional nature of fissure fills and taphonomic processes undergone by the bones before burial. Predator accumulation, reworking of remains, and geographically close fissures not being contemporaneous may account for the high diversity of the Pant-4 tetrapod fauna.

Significance of calcareous algae for the recognition of the Brigantian Stage (late Viséan) in Ireland and Great Britain

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Brigantian rocks in deep water facies in Britain have been traditionally dated with goniatites and conodonts, whereas in shallow water carbonate facies, rugose corals have been used for zonation, but these fossils have palaeoecological constraints. Foraminifera are one of the best microfaunal groups for biostratigraphic studies in shallow water facies and their utility is widely demonstrated in European Carboniferous basins. In Ireland and Britain, however, many studies have shown the limitations of using foraminifera for the Asbian-Namurian interval, because the typical European markers do not occur at the base of the different stages, or they are extremely rare, or not even recorded. On the other hand, calcareous algae have been generally ignored for biostratigraphic studies, because of mostly long-ranging taxa. The recent but progressive improvement in the knowledge of this microfloral group shows their use as biostratigraphic markers. Detailed investigations of sequences in upper Viséan rocks in Ireland suggest a distinct relay of algal genera throughout the Asbian, early Brigantian and late Brigantian. Similar assemblages of algae are recognised in northern England and Scotland. Some of the genera used for characterising biozones are: *Koninckopora, Kamaenella, Ungdarella, Coelosporella, Windsoporella, Fourstonella,* and *Calcifolium*. Comparison of Irish and British algal assemblages allows us to propose a reliable zonal scheme for shallow water facies in the late Viséan, as an alternative to the classical foraminiferal schemes.

Testing the phylogenetic relationships of 'complex' conodonts

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Evidence from the ultrastructure and soft tissues of conodonts establishes that they are vertebrates, but phylogenetic relationships within the clade remain poorly understood. The main reason for this is that most phylogenetic hypotheses have relied on two basic assumptions: the conodont fossil record is complete, and that P elements alone are sufficient for phylogenetic reconstruction. This has led to the creation of phylogenetic hypotheses through the correlation of stratigraphic occurrences. The two major classification schemes constructed to date by Sweet (1988) and Dzik (1991), show major discrepancies with respect to the division of the three orders of complex conodonts, raising the issue of one (if not both) of the schemes being inaccurate.

The central premise of this work is to elucidate the inter-relationships of prioniodontid, prioniodinid and ozarkodinid conodonts using all of the constituents of the apparatus in a cladistic analysis, thus eschewing stratigraphic data. Initial results indicate that the prioniodontids are a plesiomorphic paraphyletic group and that prioniodinids and ozarkodinids form monophyletic clades—this concurs generally with the hypothesis of relationships developed by Sweet and Donoghue (2001). The study will be extended to clarify basal relationships and those within the two more derived clades.

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Sub-fossil beetles from the Gortian interglacial site at Derrynadivva, Co. Mayo, Ireland: a palaeoenvironmental study and its stratigraphical implications

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Subfossil beetle remains from a sequence of silts and peats at Derrynadivva, Co. Mayo, Ireland provide the first known beetle assemblage of Gortian age. Although the age of the Gortian is not generally agreed upon, sites are characterised by their palaeobotanical record which suggests correlation with British interglacials showing Hoxnian-type vegetational development. Previous studies of Gortian sites record a flora without analogue today, including highly Atlantic species presently distributed in Ireland and northern Iberia but not Britain, as well as thermophilous species from southern and eastern Europe/western Asia.

The beetles as proxy indicators provide detailed information on the local palaeoenvironment and climate, indicating that at Derrynadivva, summer temperatures were slightly warmer and winter temperatures slightly colder than those of Ireland today although the climate was nevertheless oceanic. This would suggest a climate without modern analogue in Atlantic Europe. This climatic information also has a stratigraphical value because different interglacials show different patterns of climatic development. Of the two British interglacials showing Hoxnian-type vegetational development (OIS 9 and 11), Beetles from British OIS 9 sites indicate temperatures significantly higher than those at Derrynadivva which, if they can be extrapolated to Ireland, would suggest that Derrynadivva was not the OIS 9 interglacial, although the Gortian may conflate sites of more than one age.

Morphology, proposed life habits and phylogeny of "*Lithiotis*" facies bivalves

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Following extensive Late Triassic coral-constructed reefs and the aftermath of the Triassic-Jurassic mass extinction, Early Jurassic buildups are rare and constructed primarily by bivalves. The Pliensbachian exhibits a radiation of aberrant pterioid bivalves, the "*Lithiotis*" facies bivalves, which include: *Lithiotis problematica*, *Cochlearites loppianus*, *Gervilleioperna* sp., *Mytiloperna* sp. and *Lithioperna scutata*. These large bivalves with bizarre morphologies are ubiquitous in tropical, nearshore deposits.

Over 500 specimens of "*Lithiotis*" facies bivalves were collected from study sites (Western North America, Morocco and Italy) or observed in museum collections. Morphology, microstructure and phenotypic variability were examined for each of the "*Lithiotis*" facies bivalves. "*Lithiotis*" bivalves' life habits were assessed by field observations of various morphotypes and orientation of *in situ* specimens. The reef-building bivalves, *Lithiotis* and *Cochlearites*, have upright, stick-shaped growth forms. The other "*Lithiotis*" facies bivalves, *Lithioperna*, *Mytiloperna* and *Gervilleioperna* lived in lagoonal facies and exhibit a variety of morphotypes. All five "*Lithiotis*" facies bivalves share microstructures and ligament arrangements common to the pterioid families Isognomidae and the Bakevellidae. *Mytiloperna*, *Gervilleioperna* and *Lithioperna* have a broad-tooth plate and byssal attachment, characteristics of the Bakevellidae. However, *Lithiotis* and *Cochlearites* lack these traits. A phylogenetic analysis proposes that "*Lithiotis*" facies bivalves are a paraphyletic group.

Miocene cold seep communities from the Caribbean region

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Miocene aged cold seep communities have been discovered in the Caribbean islands of Barbados, Trinidad and the Caribbean coast of Venezuela. These communities contain fossil representatives of taxonomic groups characteristic of modern and other Cenozoic cold seeps, including tube worms, nuculanid, vesicomyid, mytilid, lucinid, thyasirid and solemyid bivalves, and provannid gastropods, as well as other taxa not known from modern seep sites (e.g. the deep-sea gastropod *Abyssochrysos*). The vast majority of these fossils are presently undescribed. Work over the next few years will involve thorough taxonomic and palaeoecological analysis of the Caribbean Miocene seep fossils, with the aim of investigating the origin of the cold seep communities in the Gulf of Mexico and Caribbean/western Atlantic region, and whether cold seep faunas of the Pacific and Caribbean/western Atlantic were linked and shared species prior to the raising of the Isthmus of Panama.

An exceptionally preserved biota from Upper Silurian submarine channel deposits, Welsh Borderland

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An exceptionally preserved biota of Upper Silurian (Ludlow Series) age is found in Lower Leintwardine Formation Channel fill deposits around Leintwardine in the Central Welsh Borderland. There are six submarine channels in total, although only four outcrop and yield fossil faunas. The deposits are of special importance as they represent a rare example of exceptional preservation in organisms of Silurian age; they also provide a unique palaeoenvironmental setting. The fauna is diverse, containing common representatives of Silurian biotas (such as brachiopods and trilobites), along with more unusual forms such as ophiuroid and asteroid seastars, eurypterids, xiphosurids and phyllocarids. The degree of invertebrate disarticulation varies throughout the fauna; the echinoderms are mostly complete, whilst the majority of the arthropod material is made up of disarticulated components. Specimens are predominately preserved as hard-parts, although occasional soft-body preservation is encountered in the form of rare "worm" fossils. In addition to the dominant invertebrate fauna, relatively rare disarticulated components of heterostracan fish are found; the sole taxon found, *Archaegonaspis ludensis* (Salter, 1859) is the earliest known British species of its Order. The most fossiliferous channel is that at Church Hill, which has yielded 80% of the total fauna so far studied.

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An Assemblage of the Carboniferous trilobite *Paladin mucronatus* (M'Coy, 1844)

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The trilobite Paladin mucronatus (M'Coy, 1844) has been frequently noted in marine Brigantian and Pendleian strata spanning the Lower and Upper Carboniferous boundary in northern Britain and corresponding deposits elsewhere in Europe. A pygidium, clearly assignable to the species, from Northumberland was figured as early as 1837, but despite many subsequent records few detailed studies of the trilobite have been made and as yet no ontogeny for it produced. A rich assemblage of P. mucronatus fragments, from an exposure of Lower Carboniferous Brigantian Yoredale facies marine shales at Carpley Green, near Bainbridge, Wensleydale, is illustrated, and the problems of constructing an ontogeny from incomplete poorly preserved trilobite material briefly discussed.

Reconstructing polar forest-climate dynamics from fossil wood and computer models

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Climate models used to simulate past climates have commonly prescribed the polar regions as ice-covered. However, for most of the geological past, high-latitude regions were covered by dark dense forests. These forests would have significantly modified both the polar and global climate due to their low albedo and their effect on the land-surface heat budget and hydrological cycle.

Fossil wood is abundant in many high-latitude sedimentary sequences, representing the remains of forest vegetation that once thrived in polar regions in past greenhouse climates. These forests are being studied to determine their geographical distribution, their botanical composition and their techniques for survival in the unusual polar light regime. Their leaf life span (evergreen versus deciduousness) may have been a critical adaptation for their survival and an important contribution to the local carbon cycle. Reconstructions of palaeovegetation maps and forest growth dynamics will be used to constrain simulations from vegetation and GCM palaeoclimate models for Cretaceous and Tertiary times.

An unusual deep-water fauna from the Silurian rocks of the west of Ireland

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Abundant and diverse shelly faunas have been known for over a century from the Upper Llandovery Finny School beds (upper Telychian) on the Kilbride Peninsula, western Ireland. Only recently have the stratigraphical relationships between many of these faunal assemblages been clarified. Mass mortality horizons, dominated by a range of tabulate corals, are associated with volcaniclastics and occasional bentonites in the upper part of the Finny School beds. Overlying these beds is an unusual assemblage dominated by abundant, long stems of a new species of the crinoid *Segmentocolumnus* (col.); taphonomic study suggests some postmortem reworking of the fauna by weak, low-velocity currents. The remainder of the assemblage includes a relatively diverse assemblage of brachiopods dominated by *Atrypa*, *Clorinda*, *Dolerorthis* and *Lingulella* together with matlike tabulate corals. Rarer components of the fauna include bryozoans, trilobites and dendroid graptolites. A deep-water setting is confirmed in the overlying red mudstones of the Tonalee Formation by the presence of a marginal-*Clorinda* type assemblage, dominated by *Dicoelosia*. No comparable assemblages have been reported elsewhere from the Midland Valley of Scotland and its Irish counterparts. The biota may have represented a response to a peculiar, deep-water environment periodically charged with the distal flows of volcaniclastic surges.

Late Neogene dinoflagellates and sequence stratigraphy of the Southern North Sea Basin

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The correlation of Upper Cenozoic marine deposits across the southern North Sea basin has been fraught with difficulties. However, dinoflagellate cysts and marine acritarchs are shown to be useful for the correlation and environmental reconstruction of these deposits, owing to their wide salinity tolerance, high taxonomic diversity (more than 100 taxa), and good preservational potential. In eastern England only the Pliocene and lower Pleistocene are represented substantially by marine deposits, and even here the record is highly incomplete. Dinoflagellates help constrain the age of these deposits. In northern Belgium, Neogene marine deposits represent the southeastern margin of the southern North Sea Basin. These deposits are also discontinuous, but include the lower, middle and upper Miocene as well as lower and

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upper Pliocene. The Miocene and lower Pliocene dinoflagellate assemblages are particularly diverse and well preserved, and facilitate correlation across the North Atlantic and as far as the US Atlantic coastal plain and shelf. The Pliocene assemblages can be correlated with those of eastern England and into the North Atlantic.

We present a biostratigraphic synthesis for the southern North Sea Basin and attempt to reconcile the stratigraphy of this region with the sequence chronostratigraphic framework of Hardenbol *et al.* (1998).

Angiospermid pollen from the Middle Triassic: Morphology, biostratigraphy and possible affinity

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Middle Triassic sediments of the Barents Sea area contain a variety of dispersed colpate, and operculate pollen grains of angiospermid morphology. Seven different pollen types can be differentiated, all from the same stratigraphic interval (Ladinian to Anisian). Due to their consistent occurrence some of them have been used as stratigraphic markers under the designation of *Retisulcites* sp. 1, 2 (Hochuli *et al.* 1989) and *Retisulcites* sp. A (Vigran *et al.* 1998). All the described forms are characterised by well-developed semitectate reticulate sexines, which are connected by columellar structures to thin nexines (footlayer and endexine). Due to the pollen's very small size, their microscopical analysis is near the limit of optical resolution. So, in addition to high-resolution transmitted light microscopy, Confocal Laser Scanning Microscopy (CLSM) has been used for morphological analysis of the very delicate wall and surface structures. In CLSM the specimens were imaged in very thin, only ca. 360 nm thick, optical sections using fluorescence mode (excitation 568 nm, detection 590 nm LP). The optical sections were subsequently re-composed to generate extended focus images and 3D computer models. Pollen grains of comparable morphologies are common in sediments of Early Cretaceous age (Aptian / Albian). For the Middle Triassic all these pollen types are new; some of them show resemblance to the forms described by Cornet (1989) from the Carnian of the Richmond Basin (VA, USA). In the Barents Sea area the consistent occurrence of these angiospermid pollen shows that the producing (mother) plants were widely distributed and their diversity suggests that several species were involved. Among modern angiosperms reticulate, monocolpate pollen are generally associated with magnoliid affinity, however, it cannot be excluded that these pollen represent a so far unknown group of gymnosperms which produced pollen of angiospermid morphologies.

The ancestry of priapulid body plan

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The priapulid worms form a small ecdysozoan phylum with only 17 species living in present-day marine environments. Fossil evidence indicates that they were important elements of the endobenthic communities in the Early and Middle Cambrian but the evolutionary relationships of modern priapulid lineage to their Cambrian ancestors have so far never been resolved. Current studies of priapulids in the Early Cambrian Maotianshan Shale (SW China) bring new information on the ancestry of the priapulid body plan.

1. Early Cambrian priapulids are diverse with at least four different lineages (Acosmiidae, Corynetidae-Anningidae, Selkirkiidae and Palaeoscolecida) all characterised by distinctive features of their body plan
2. Some key-features of the body plan of modern priapulids such as the pentagonal arrangement of circum-oral teeth and the caudal appendage are recognised in the Early Cambrian priapulid *Anningia*
3. A new (extinct) body plan of particular evolutionary significance is represented by the Corynetidae-Anningidae (smooth contracted introvert)
4. *Acosmia* and *Xiaoheiqingella* may represent the ancestral body plan (swollen introvert bearing scalids, caudal appendage) from which modern Priapulidae derived.

Palaeoecological zonation in crinoids from marginal marine environments in the Bathonian of Central and Southern England

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New research into the palaeoecology of echinoderms has demonstrated a lack of understanding of their environmental palaeoecology. This is in part due to taxonomy being based on exceptionally preserved whole specimens and not single ossicles whose affinity is problematic, in addition to the general absence of studies of echinoderms from facies lacking entire tests. Thus it has become necessary to consider fragmentary remains in defining a more representative palaeoecology. Bulk sampling (10 to 40 kg) of the Bathonian sediments of England, where marine environments ranging from open shelf to lagoon are represented, has revealed members of echinoderm groups inhabiting a full range of environments/salinity conditions. Extensive work on exceptionally preserved Middle Jurassic crinoids from Northern Switzerland and the British Liassic has enabled identification of crinoid columnals from the English Bathonian to generic level, thus allowing the community structure of the crinoids to be exemplified within

clearly defined ecosystems delineated by facies and degree of marine connection. Results indicate distinct crinoid communities based on the presence and absence of generic indicators. Examples include smaller forms, e.g. *Chariocrinus* and *Balanocrinus* inhabiting fully marine conditions, while larger *Millericrinus* and *Ailsacrinus* have been found inhabiting the carbonate shelf. *Pentacrinites* appears to inhabit the oolite shoal. *Isocrinus* on the other hand, is found to predominate in lagoons, but only up to a marked ecological cut off point, defined by low salinity/low oxygen conditions.

Ontogenetic variation in the frog ilium and its impact on classification

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Anurans are a successful group of vertebrates comprising around 4,000 extant species. Their fossil record extends back to the Early Jurassic. Most fossils are preserved in one of three ways: impressions, articulated skeletons, and disarticulated 3-D elements from microvertebrate localities. In the latter case, new taxa are often diagnosed and described on the basis of ilia. Common diagnostic features include: the shape and size of the acetabulum, superior iliac tuberosity, and dorsal crest, and the prominence of the partes ascendens and descendens. However sample size is often small and we need to ascertain whether any observed variation is phylogenetically significant or due to individual differences (e.g. ontogeny, sexual dimorphism). In order to evaluate the importance of ontogeny on iliac form, we examined growth series for two anuran species, *Bufo punctatus* (Bufonidae) and *Hyla regillia* (Hylidae). Most of the commonly used diagnostic features did not change substantially. However, in *B. punctatus*, the shape of the dorsal tubercle and the relative height of the acetabulum varied to some degree, while in *H. regillia* changes were more subtle and involved the prominence of crests and depressions. In addition, the angle of the iliac shaft altered with maturity in both taxa.

A spinosaurid furcula and its phylogentic implications

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Furculae (fused clavicles) have been identified in several groups of theropod dinosaurs, including allosaurids, tyrannosaurids, oviraptorids, therizinosaurids, dromaeosaurids, troodontids, and herein the spinosaurids. A recently discovered skeleton of the African spinosaurid *Suchomimus tenerensis* confirms the presence of an ossified furcula and suggests that this fused bone characterized the earliest tetanurans. Indeed, the very recent report of furculae in coelophysoids (*Syntarsus, Segisaurus*) that are Early Jurassic age suggest a Triassic origin among basal neotheropods. The condition in neotheropod outgroups is uncertain for herrerasaurids, but an ossified furcula is not present in the basal theropod *Eoraptor*. Preservational bias has played a dramatic role in questioning the near universal presence of this fused bone in neotheropods.

The flattened, V-shaped bone has a width of approximately 31 cm and has a short, tongue-shaped hypocleideum approximately 2 cm in length. An elliptical scar about 8 cm in length is present at the distal end of each epicleideal ramus for attachment to the anterior margin of the coracoid and acromion. The intrafurcular angle is 111 degrees. The furcula closely resembles that of *Allosaurus*.

Sereno *et al.* (1998) initially described *S. tenerensis* from a partial skeleton from the Lower Cretaceous (Aptian), Elrhaz Formation, Gadoufaoua, Niger, Africa. In 2000, a nearly complete postcranial skeleton was recovered that included a furcula. Prior to this find and the recent report of coelophysoid furculae, the most primitive tetanuran furcula was that of *Allosaurus*.

Age and palaeoenvironments of a shallow marine Pliocene sequence in northern Belgium revealed by dinoflagellate cyst stratigraphy

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The subsurface Pliocene of northern Belgium was deposited in a shallow marine environment at the southern margin of the North Sea Basin. Basal gravel lags and characteristic lithologies permitted a robust lithostratigraphic subdivision in the 1970s, but correlation with the sequence chronstratigraphic framework of Hardenbol *et al*. (1998) remained incomplete owing to imprecise biostratigraphic control. The effects of deposition under a varying sea level regime in a marginal marine environment are clearly observed in the Pliocene by distinct and rapid facies variations. Well-preserved dinocyst assemblages were recovered from a Pliocene deposit in two temporary exposures in Antwerp harbour. These assemblages reflect age, depositonal environment, and climatic events.

The dinocyst assemblages from the Kattendijk Sands point to deposition under warm-temperate conditions in open waters during early Pliocene times. A correlation of the lower boundary with sequence boundary Me2 is proposed. Cooling associated with the overlying Luchtbal Sands persists into the base of the transgressive Oorderen Sands, after which mild conditions were reestablished. An uppermost clayey unit here identified as the Kruisschans Sands announces a shallowing of the depositional environment. Dinoflagellate evidence indicates that the Kruisschans Sands predate northern hemisphere glaciation at 2.6 Ma.

Silurian thelodonts from the Welsh Borderland and co-occurrence with conodonts

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New data on thelodonts from the Middle Llandovery-lowermost Lochkovian of the Welsh Borderland are presented as well as the distribution of co-occurring conodonts. Thelodonts are rare in the Llandovery and Wenlock Series. Like the Wenlock, the basal part of the Ludlow Series is mostly barren of thelodonts but small numbers of the important species *Paralogania martinssoni* and *Thelodus laevis* are present with long ranging conodont species of *Ozarkodina* and *Panderodus*. In the uppermost part of the Upper Bringewood Formation, *Paralogania kaarmisensis* and *Phlebolepis elegans* have been recovered together with the zonal conodont *Polygnathoides siluricus* (P.C.J. Donoghue and R.E. Elliott *pers. comm.*). The Whitcliffe Formation, uppermost Ludfordian, provides the most diverse and well-preserved material.

Frequent *Thelodus parvidens* and *Thelodus trilobatus* occur in association with the rarer zonal conodonts *Ozarkodina snajdri*, *Ozarkodina crispa* and *Ozarkodina remscheidensis eosteinhornensis*. At the base of the Prídolí Series there is a change to a thelodont fauna dominated by *Paralogania ludlowiensis*, which first appears at this level, in association with *Nethertonodus prodigialis*. Higher in the Prídolí Series, a succession of thelodont faunas including *Katoporodus* ?*timanicus*, *Goniporus alatus*, *Paralogania kummerowi* ssp. 1, *P. kummerowi* ssp. 2 and ?*Loganellia unispinata* can be traced before the incoming of the lowermost Devonian taxon *Turinia pagei* along with *Nikolivia toombsi*. Similarities in thelodont faunas between the Welsh Borderland and the Baltic are presented, showing new correlations in the lower part of the Ludlow Series and uppermost Prídolí Series, where zonal conodont species are extremely rare or absent in Britain.

Quantitative vertebrate palaeocommunity analysis – A realistic goal?

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The application of modern statistical techniques to palaeoecology allows quantification of what has previously been a very scenario-driven branch of palaeontology. Given these techniques, which aspects and to what degree can vertebrate palaeocommunities be accurately reconstructed, if at all? Many recent analyses use simple species lists to describe palaeocommunities. More useful than this is an appreciation of the abundances of those organisms present, as not only does it reflect ecological dominance but also illustrates finer scale variability in ecosystem composition. Several conditions must be met by the analysed community in order for there to be any chance of relative abundance being preserved; the community must have been stable for a significant period of geological time (>100 ka), taphonomic and taxonomic biases must have been constant or predictably varying and fossils must be present from a wide range of facies. Accurate community analysis also requires a change in sampling protocol as many vertebrate fossil deposits represent catastrophic events which should not be included in abundance analyses. I attempt to model this using a C++ program written for the purpose, incorporating the effects of sampling as well as the effects of biases on the final community composition in order to demonstrate whether it is possible to make any reconstruction of relative abundance in vertebrate palaeocommunities.

New synziphosurines from the Lower Silurian of Wisconsin

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Synziphosurines are a primitive group of paraphyletic Xiphosura (Chelicerata), with a reliable fossil record from the Mid Silurian to the Late Devonian. New synziphosurines, represented by approximately ten specimens, attributable to at least two new taxa, are described from the Llandovery Waukesha Konservat-Lagerstätte of Wisconsin, U.S.A. They form part of an unusual assemblage including trilobites, phyllocarids, ostracods, thylacocephalans and a myriapod, which lacks shelly faunas typical of regional carbonate deposits. The new synziphosurine material preserves their prosomal appendages, which are extremely rare amongst this group, only previously described from *Weinbergina optzi*, from the Devonian Hünsruck Slate. This material therefore extends the known fossil record of synziphosurines back to the Lower Silurian and provides additional morphological characters which are important in elucidating the complex evolutionary history of primitive Chelicerata.

Late Wenlock Graptolites from near Orange, New South Wales

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Assemblages of graptolites from sections at One Tree Hill and Wallace Creek are described. The Wallace Creek specimens come from the *lundgreni* zone. A possible faecal pellet made up of individuals of *Monograptus testis* (Barrande 1850) was found at one locality. Most of the One Tree Hill specimens come from the *praedeubeli-deubeli* zone, the zone succeeding the *lundgreni-testis* zone. The fauna includes several species of retiolitid, *Colonograptus ludensis* (Murchison 1839) and *Monograptus insperatus* Koren' 1992. This is the first record of *Monograptus insperatus* from New South Wales and the second outside central Asia. This has implications for graptoloid biogeography after the *lundgreni* event, implying a faunal connection between central Asia and Australia at this time.

A Lower Carboniferous sipunculan from the Granton Shrimp Bed, Edinburgh

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The Granton Shrimp Bed is a Konservat-Lagerstätte, with a restricted biota including abundant arthropods, and rare polychaete worms, nautiloids, conodont animals and problematica. Here we describe a specimen of a sipunculan from this locality. Sipunculans (Phylum Sipuncula) are sedentary marine worms with a partly evertible trunk, believed to represent an early coelomate grade, probably with a close relationship to the annelids. They are unmineralised and extremely rare in the fossil record; poorly preserved specimens would also be difficult to recognise, since they possess few distinguishing features. Identification in this case relies largely on the arrangement of transverse and longitudinal wrinkling of the cuticle, reflecting the distinctive underlying musculature. The present specimen shows close similarity to *Lecthaylus gregarius* Weller, 1925, from the Silurian of Illinois, and is referred to that genus. This is the first known fossil sipunculan from the Carboniferous, or from the UK.

A new dipnoan fish from the Middle Devonian of Scotland and its importance to the evolution of the dipnoans

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In the last century Ramsey Traquair (1914) described specimens of the Devonian lungfish *Pentlandia macroptera* as existing in the area of Baligill, Sutherland, Scotland. Later Miles and Westoll (1963) could not find the specimens referred to by Traquair and put the Baligill deposits at the Eifelian horizon, well below the Givetian where all specimens of *P. macroptera* have previously been found. New specimens with a superficial resemblance to *P. macroptera* have been discovered by the authors from Baligill and elsewhere. Also, specimens probably used by Traquair in his identification of *P. macroptera* have been found housed in the National Museums of Scotland which belong to the new species. The new species, *Balipinnalatus saxoni*, shows primitive characteristics of the skull but also advanced characteristics of the post cranial body. This is important to the recognised textbook evolution of the dipnoans.

The Middle Oxfordian ammonite faunas of Upware, Cambridgeshire, eastern England—a remarkable bridge between Boreal and Tethyan realms

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Substantial new exposures of Middle Oxfordian limestones and marls at Upware, Cambridgeshire (eastern England), have yielded an unusually diverse ammonite fauna, including Boreal Cardioceratidae and Tethyan Perisphinctinae, often in almost equal proportions. The sequence of species of *Cardioceras* demonstrates a gradual change in the proportion of morphospecies present with time through the uppermost Densiplicatum (fauna I) and into the Tenuiserratum chronozones (faunas II-IV). Perisphinctidae show more radical changes, however, from regularly ribbed *Arisphinctes* (with "*Otosphinctes*" microconchs; faunas I-II) to strongly variocostate *Perisphinctes* sensu stricto (with *Dichotomosphinctes* microconchs; faunas III-IV). This change corresponds to the Submediterranean Plicatilis-Transversarium chronozone boundary—for the first time the position of this change, which can be recognised over much of Europe, can be established within a Boreal cardioceratid zonal scheme, and lies *within* the Tenuiserratum Subchronozone (Tenuiserratum Chronozone). Occasional records of the Tethyan Aspidoceratinae and Ochetoceratinae provide useful additional comparisons with the faunas of southern areas. As the sequence of faunas at Upware has great potential to link Submediterranean and Boreal province successions precisely, a sequence of biohorizons is proposed: aff. *pickeringius* (I), aff. *maximus-sopotense* (II), *antecedens* (III), *parandieri–tenuiserratum* (IV).

The Upware locality will be visited by the Association during the conference field excursion.

Quaternary Land Snails from Tenerife; Clues to the Palaeoclimate?

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Tenerife, situated approximately 150 km off the west coast of Africa, is the largest island in the Canarian archipelago and originated by hotspot volcanism over a slow-moving oceanic plate. Pumice fall deposits, ash layers and ignimbrites preserve a record of some of the eruptions. The Bandas del Sur formation, the most well researched sequence, occurs in the south east of the island and Argon/Argon dating of sanidine crystals from the pumice fall deposits has produced dates for six of the eruptions dated back approximately 600,000 years. Pumice fall deposits contain a record of organisms within and on the soil surface at the time of the eruptions and commonly contain land snail shells. Dating of the deposits provides a stratigraphic constraint for the snails that can be superimposed on the marine oxygen isotope curve to infer the temperatures at the time. Land snail shells are composed of calcium carbonate that has a carbon and oxygen isotope composition determined by diet, atmospheric CO_2 and precipitation. Future stable isotope studies of the snail shell carbonate will enhance the marine core data by suggesting the palaeo-vegetation, precipitation and temperatures. This poster aims to link the various data to reconstruct the Quaternary palaeoclimate.

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The morphology and phylogenetic position of the enigmatic, extinct arachnid order Phalangiotarbida

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Phalangiotarbids are an order of extinct, enigmatic arachnids that have been found only in the Early Devonian of Germany and the Coal Measures of North America and Europe. They are characterized by a single median ocular tubercle bearing six eye lenses, a broad prosoma-opisthosoma junction, six abbreviated anterior tergites, four larger posterior opisthosomal tergites and a dorsal anal operculum. This study of the abundant *Phalangiotarbus subovalis* material from the Upper Carboniferous of Writhlington, Somerset, UK, reveals new information about the morphology of the apotele (i.e. the distal podomere of the walking legs), the fifth sternite, the opisthosomal segmentation, and confirms the anal operculum as a dorsal feature.

Their phylogenetic affinities are obscure. They have been claimed to have close affinities with Opiliones, Acari, Pedipalpi and Amblypygi. A new comprehensive cladistic analysis, based on sixty-four characters of thirteen terminal arachnid taxa (plus a hypothetical outgroup), resolves Phalangiotarbida as sister-group to Palpigradi + Tetrapulmonata. A 'fossil-friendly' approach, whereby those characters that could only be coded in extant taxa are excluded from the analysis, produces a strict consensus tree that shows Phalangiotarbida placed in an unresolved clade with Ricinulei, Acari, Palpigradi, Araneae and Trigonotarbida, and basal to the other tetrapulmonata taxa. The topologies recovered from both approaches are, thus, broadly congruent.

The Lilliput Effect in the aftermath of the end-Permian extinction event

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Fossil organisms in the immediate aftermath of extinction events are much smaller than in the pre-extinction fauna (the Lilliput effect). The cause(s) of this phenomenon remain unknown. Is it due to a disappearance of large taxa, the appearance of many small (opportunist?) taxa, or a general dwarfism affecting the whole fauna?

We present the first quantitative study of within-lineage size decrease, and subsequent increase, through the Permian-Triassic (P-Tr) extinction and recovery interval. Four unrelated taxa were studied from P-Tr sections of Europe. *Bellerophon* and *Lingula* both pass through the P-Tr event. The mean size of Late Permian *Bellerophon* and *Lingula* is 17 mm and 5 mm respectively. Both taxa are much smaller in the Early Griesbachian (*parvus* Zone): mean lengths 5 and 3 mm respectively. A return to pre-event size took place in the later Griesbachian (*carinata* Zone). The bivalves *Unionites* and *Claraia* are also very small in the Early Griesbachian (4 and 7 mm respectively), before also increasing in size in the *carinata* Zone (18 and 24 mm). All differences are statistically significant. Size decrease is clearly temporary, and affects all taxa equally, suggesting a phenotypic response to environmental change such as a period of reduced food supply.

Natural assemblages of *Idioprioniodus* (Conodonta, Vertebrata) and the first accurate three-dimensional skeletal model of a prioniodinid conodont

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Without natural assemblages preserving articulated skeletons, our understanding of conodonts would be radically different. Hypotheses of multielement composition, apparatus architecture, element homology, phylogenetic relationship, and taxonomic assignment all ultimately rest on data derived from natural assemblages.

Conodonts assigned to the Family Prioniodinida, especially those from the Late Palaeozoic, provide clear examples of the difficulties in dealing with groups of conodonts for which natural assemblages are unknown. In this context, species of *Idioprioniodus* are important as they may constitute the stem lineage from which many late Palaeozoic and Triassic prioniodinids evolved. But there is no agreement concerning the homologies of the elements in the apparatus, and as a result analysis of the evolutionary relationships of *Idioprioniodus* is problematic, to say the least.

We have discovered two specimens that preserve articulated remains of *Idioprioniodus* and from these we have produced a 3D model of the apparatus. The model confirms that the architecture of prioniodinid conodonts was essentially the same as that of the better known ozarkodinid conodonts, but highlights a number of differences and difficulties, particularly concerning the orientation of digyrate elements in S and P positions. Notwithstanding these difficulties, knowledge of the 3D architecture of *Idioprioniodus* and direct evidence for topological homology of the elements will provide a more secure framework for reconstruction and phylogenetic analysis of problematic Late Palaeozoic prioniodinids.

Devonian ichthyoliths from northern Spain (Asturias) and northern Italy (Carnic Alps): a Gondwana–Euramerica connection

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During the Devonian, southern Europe occupied a privileged situation for the study of relationships between Euramerica and Gondwana because of its location between both continents. Vertebrate microremains have been poorly studied in this region. Gnathostome ichthyoliths from the Devonian of northern Spain (Asturias) and northern Italy (Carnic Alps) are described; they complement data from other Spanish regions and give a first idea of the Italian fauna. 49 placodermes, chondrichthyans, acanthodians, actinopterygians and sarcopterygians taxa are described morphologically. Emsian acanthodians predominate in the Spanish fauna whereas Famennian chondrichthyans predominate in the Italian fauna. The stratigraphical

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distribution of studied taxa is established for both regions. The palaeobiogeographical distribution of these vertebrate faunas is located within the intertropical zone and affinities are shown for Gondwana as well as for Euramerica. The Carnic Alps late Famennian assemblage seems to be equivalent to the *Phoebodus* biofacies (*sensu* Ginter), but it differs from it by the occurrence of *Siamodus*, which suggests a new definition of late Famennian chondrichthyan biofacies.

Lower Palaeogene microfossil biostratigraphy of the Davis Strait, offshore West Greenland

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Microfossils from the Palaeocene and Early Eocene succession from the Davis Strait, offshore West Greenland have been investigated. The study concentrated especially on foraminiferids but diatoms, radiolarians and other fossil groups were also analysed. In general, the five boreholes contained fairly well preserved and diverse faunas and floras, but the diversity and density varied significantly both laterally and stratigraphically. The studied interval was subdivided into three foraminiferid biostratigraphic intervals, in ascending stratigraphic order, the *Stensioeina beccariiformis*, *Praeglobobulimina ovata* and *Pseudohastigerina wilcoxensis* intervals, and five biostratigraphic intervals based on additional microfossil groups (the *Thalassiosiropsis wittiana*, *Fenestrella antiqua-Coscinodiscus morsianus*, Ostracod, *Aulacodiscus hirtus* and *Cenodiscus-Cenosphaera* intervals). In most cases, it was possible to correlate the biostratigraphic intervals with the existing zonations of the Labrador Sea.

Carbonate depositional environments and their influence on exceptional preservation in the Much Wenlock Limestone Formation of Dudley, England

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The Much Wenlock Limestone Formation (Silurian), exposed near the town of Dudley, England, contains one of the richest known Silurian carbonate faunas. Over 600 species representing nearly 30 taxonomic groups are known from the Dudley inliers, and for many species, Dudley represents the type locality. The exceptional preservation and diversity of the fossil biota, in particular pelmatozoan echinoderms and trilobites, has been the object of scientific inquiry since the late seventeenth century. Yet in spite of much scientific interest relatively little is known as to their precise stratigraphic distribution and faunal/sedimentological associations.

This study is based upon comparisons between outcrop and museum collections and has identified a number of stratigraphic discriminators that allow the identification of the intervals from which much of the Dudley material originated. Exceptional preservation appears to be restricted to those sediments deposited between SWB and FWWB and has been further enhanced during periods of transgression. Thus the identification of the horizons from which the Dudley collections originated allows fresh insights into the palaeoecology and taphonomy of the Much Wenlock Limestone Formation.

Taphonomy of larger benthic foraminifera and its relevance for the interpretation of the fossil record

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Larger foraminifera occur on carbonate platforms and reefs. The stratigraphy of this type of environment is largely based on the occurrence of larger foraminifera, because of their relatively rapid evolution. Less attention has been paid to the ecological importance of benthic foraminifera though. In this study I compared the distribution of living benthic foraminifera shelf with the distribution of empty tests. The study was performed on the Spermonde Shelf (SW Sulawesi). Species living on the reefs are poorly represented in the fossil record, whereas species living on the reef base and further from the reefs are better preserved. The latter group turned out to be also the best group to represent environmental parameters.

Jurassic dinosaur tracks and communities from the Cleveland Basin, Yorkshire: the story nine years on

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Work carried out by the authors since 'Pal. Ass. 1993' has led us to believe that dinosaur tracks characterize the non-marine Middle Jurassic sequences exposed along the 55 km stretch of coast between Filey and Staithes, Yorkshire. Nearly 30 different track morphotypes have now been recognized. These may be readily categorized into three major groups; (a) large tracks made by habitual quadrupeds, (b) tridactyl tracks made by habitual bipeds, and (c) tracks consisting of essentially parallel digit imprints, resulting from a swimming behaviour. The validity of these morphotypes will be discussed in terms of whether they are distinct ichnotaxa; or if they may represent preservational variants, ontogenetic growth series or sexual dimorphs. Our present conclusions indicate that the track morphotypes possibly represent at least 15 ichnotaxa. These ichnotaxa in turn were probably made by some 10 species of dinosaur. Although it is not possible at present to postulate distinct dinosaur communities throughout the Middle Jurassic of Yorkshire, we are in a position to present a 'combined' community that inhabited the coastal plain complex of the Cleveland Basin.

All done without the use of bones!

posters

Fine-scale variants of the Haptophyte alga *Calcidiscus leptoporus*: 'Cryptic' species or ecophenomorphs?

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The cosmopolitan coccolithophorid *Calcidiscus leptoporus* has long been thought to exemplify the phenomenon of fine-scale speciation (an evolutionary mechanism giving rise to groups of weakly divergent morphotypes, traditionally bracketed as single species, which can in fact be separated on the basis of consistently expressed recondite morphological differences). However, the validation of such a model is contingent on the successful discrimination of 'true' genetic variation from background ecophenotypic morphological responses. This study has utilised cultured strains of *C. leptoporus*, grown across a range of temperatures (13-23ºC) and subsequently analysed using semi-automated morphometrics, as a means of evaluating the relative importance of environmentally mediated plasticity and genetically controlled morphological variation. The two strains analysed grouped consistently (although with some overlap) into disparate regions of a two-dimensional morphospace field (defined by two independent measurements of distal shield diameter), one around a mean of 6.09µm (corresponding to the 'Intermediate' morphotype of Knappertsbusch *et al.* 1997), the other with a mean of 8.64µm (equivalent to their 'Large' morphotype). Although a weak ecophenotypic overprint may be present, expressed morphology is largely unaffected by temperature. A series of spontaneous heterococcolith-holococcolith phase-changes in monoclonal populations confers increased confidence that *C. leptoporus* 'Intermediate' is exclusively associated with the holococcolith *Crystallolithus rigidus*, further reinforcing interpretation of morphological variation within the *C. leptoporus* concept as a result of evolutionary processes.

Neglected Girvan molluscs muscle in on Ordovician biodiversity patterns

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The Ordovician successions of the Girvan district, SW Scotland are well suited for the study of regional scale changes in the whole fauna during the global diversification event. They represent a wide range of shelf and upper slope environments on the Midland Valley Terrane, close to the Laurentian margin. Some groups, including brachiopods and trilobites, are well documented but others, including, rare and problematic taxa, have long been neglected. Detailed sampling and examination of museum collections suggest that these groups are more abundant and diverse than the literature indicates. Their analysis is therefore important if changes in overall biodiversity and palaeoecology are to be understood.

The molluscs are amongst these neglected groups. Recent sampling has revealed bivalves from the uppermost Llanvirn–lower Caradoc in both nearshore and offshore facies. These may be amongst the earliest bivalves to reach the Lauentian margin, following their early Ordovician diversification in Gondwana. They occur with greater diversity, abundance and variety of mode of life in the upper Caradoc and Ashgill faunas. Cephalopods, polyplacophorans, 'monoplacophorans', rostroconchs and gastropods are present throughout the succession, with gastropods in particular being ubiquitous across the entire spectrum of environments, although some genera are more restricted in habitat type.

Depositional depth estimation and the bathymetric distributions of modern populations of some common Neogene Bryozoa from New Zealand

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Estimates of depositional depth are routinely sought by geologists. Fossils of extant species provide one method of inferring palaeodepth using depth ranges of present-day populations. This method has not been adequately tested for bryozoans because of the paucity of comprehensive data on the depth ranges of modern species. Bryozoans are among the most abundant benthic animals living on the continental shelf around New Zealand. Here we test their utility in palaeodepth estimation by recording the bathymetric distributions of four distinctive endemic species—*Cinctipora elegans*, *Attinopora zealandica*, *Diaperoecia purpurascens* and *Celleporaria emancipata*—all of which are commonly found in the Neogene of New Zealand. A survey of the extensive collections of the New Zealand Oceanographic Institute, comprising more than 9,000 benthic stations, revealed very wide bathymetric ranges: 17-914 m for *C. elegans*, 35-1156 m for *A. zealandica*, 0-1156 m for *D. purpurascens*, and 68-690 m for *C. emancipata*. There is little scope therefore for applying these four bryozoan species in palaeodepth estimation. More general problems in using azooxanthellate benthic animals to infer depositional depth are highlighted.

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The first Silurian chasmataspid (Chelicerata: Chasmataspidida) from Lesmahagow, Scotland, and phylogenetic implications for eurypterids

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A new chasmataspid (Chelicerata: Chasmataspidida) is described from the Early Silurian (Late Llandovery–Early Wenlock) of Lesmahagow, Scotland. It is distinguished from related forms by the low tapering ratio of the postabdomen and a heart-shaped metastoma. It is the first Silurian chasmataspid to be described from the fossil record and bridges some of the morphological gap between the Ordovician Chasmataspididae and the Devonian Diploaspididae, and supports a monophyletic Chasmataspidida. Ventral prosomal and opisthosomal structures are described, revealing pediform prosomal appendages, a very eurypterid-like heart-shaped metastoma, a genital appendage and a three-segmented genital operculum. Chasmataspids are regarded as a primitive sister group to the eurypterids; the three-segmented genital operculum of *Dolichopterus*, and Stylonurina are considered plesiomorphic within Eurypterida, while the two-segmented genital operculum, with deltoid plates, of Eurypterina is considered apomorphic.

Biodiversity and climate change in Antarctic Palaeogene floras

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The Cenozoic was a critical period in Earth's climatic history, during which greenhouse climates of the early Palaeogene switched to the icehouse climates of today. However, as yet we know little about terrestrial environments and vegetation response at high latitudes during this time.

Some of the best preserved plant fossils of Palaeocene to Eocene age in the Southern Hemisphere were collected from Seymour Island, Antarctic Peninsula. Thirty six angiosperm leaf types have been identified, along with pteridophytes (ferns), and podocarp and araucarian conifers. Plants with affinities to living families typical of cool-warm temperate (e.g. Nothofagaceae, Proteaceae) and sub-tropical (e.g. Lauraceae, Sterculiaceae) vegetation dominate the assemblage. Quantitative analysis of these angiosperm leaves provides a mean annual temperature of 13.5 ± 0.7°C for the late Palaeocene. This warm climate was able to sustain large forests, even at such high latitudes. Younger Eocene floras show decreasing diversity and increased dominance by *Nothofagus* trees as a response to cooler, more seasonal climates (mean annual temperature 10.8°C).

A chitinozoan study in the type area of the Ashgill Series, Cumbria, UK: preliminary results

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In a recent study, Rickards (in press) has shown that the Rawtheyan Stage of the type Ashgill Series, Howgill Fells, Cautley District, is of *linearis* graptolite Biozone age, implying that the base of the Ashgill, in graptolitic terms, begins at least two graptolite zones earlier than previously supposed. A dozen samples, taken from the graptolite slabs, all originating from Ingham's (1966) zone five, six and seven within the Rawtheyan part of the Cautley Mudstone Formation, are investigated for their chitinozoan content. They yield diverse assemblages of moderately well preserved chitinozoans, including index species described before in other places on the Avalonia and Baltica palaeocontinents (e.g. *Lagenochitina baltica* and *Conochitina rugata*) as well as new species. Based on these preliminary but encouraging results, sixty more samples have been collected this summer from the upper Onnian to the lower Silurian strata from the Westerdale, Taythes and Murthwaite Inliers. They are currently being investigated, in order to produce a consistent chitinozoan biozonation in this stratigraphically important area, tied to the revised graptolite data.

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The extinction of Morozovella and calibration of some Middle and Late Eocene planktonic foraminifera bioevents to an astronomical time-scale

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New and existing planktonic foraminiferal biostratigraphic events of the late middle Eocene have been examined with a sampling resolution of ~3 kyr. These have been calibrated to an astronomical time-scale to define accurately the timing of key biostratigraphic events, particularly the extinction of *Morozovella spinulosa*, which is a distinct biomarker for late middle Eocene sediments. The final large acarininids (*Acarinina praetopilensis*) terminate 8 kyr prior to the extinction of *Morozovella spinulosa* and dwarfed acarininids continue in the smaller size fractions (<125 μm) until 36.43 Ma.

High-resolution stable isotopic analyses ($\delta^{18}O$, $\delta^{13}C$) have been conducted on planktonic foraminifera from the western North Atlantic, to reconstruct sea surface temperatures and the structure of the thermocline around this major biotic turnover. Whilst the extinction of

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Morozovella spp. and *Acarinina praetopilensis* occur during a long-term cooling trend, there is no major palaeoceanographic event associated with the extinction that can be deduced from stable isotopic analyses alone. It is concluded that the extinction of *Morozovella* spp. and the decline in the acarininid lineage was probably related to nutrification of surface waters and / or symbiont elimination.

A new gastropod fauna from the Early Triassic of Oman

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The Griesbachian (Lower Triassic) Al Jil Formation of Oman has yielded a new, rich and partially silicified gastropod fauna. These gastropods form part of a larger shallow marine assemblage, which is the only silicified Griesbachian assemblage known to date. A large proportion (69%) of Permian-Triassic gastropods are Lazarus taxa in the Griesbachian, which Erwin (1996) attributed to the absence of silicified faunas at this time. The discovery of the Oman assemblage allows us to test Erwin's hypothesis: does it contain any of the missing Lazarus taxa as predicted by the silicification hypothesis?

Ten gastropod genera are present in the fauna: *Ananias, Bellerophon, Chartronella, Coelostylina, Naticopsis, Omphaloptychia, Soleniscus, Strobeus, Worthenia,* and *Zygopleura*. It is the most diverse Griesbachian gastropod assemblage known. Two of these (*Ananias* and *Soleniscus*) were previously unknown as fossils in the Griesbachian (i.e. they represent some of the missing Lazarus taxa). Thus, while some Lazarus taxa are present, as predicted, the majority of the assemblage is composed of "typical" Griesbachian forms. There are several possible reasons for this. Our analysis raises to fifteen the total number of Griesbachian gastropod genera that are represented by actual fossils. Twenty-seven Lazarus genera remain to be found in this interval.

Stromatolite morphology controlled by flow regime: an abiogenic model

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The nature of stromatolite morphogenesis is one of the current challenges to Archaean palaeobiology. The debate is fundamental to our understanding of the evolution of early life since stromatolites at present provide the oldest evidence for life on Earth. The question is whether stromatolites inherently require a biological community in order to form, or if they can be generated by physical and chemical processes alone. If it can be shown that the existence of stromatolites does not obligate the existence of life then a serious review of our current stance on early life is in order. The issue also has great implications for the search for the evidence of life on Mars.

New experimental techniques, using spray paint as a suitable analogue to the sedimentary environment, have been applied to the problem in order to enhance our understanding of the generation of stromatolite morphologies. Stromatolitic fabrics were successfully produced and found to occur in zones linked to different flow regimes. A new model incorporating the effects of flow regime and viscosity governed by the Mullins-Sekerka Instability is proposed and, although it does not exclude the interaction of microbial organisms in the construction of stromatolite morphologies, it discards the necessity for a biological input therefore placing doubt on the biological nature of many ancient stromatolites, and calls into question our understanding of early life on Earth.

Radiolarians and conodonts from radiolarites in NW-Thailand; witnesses of a 140 my (at least) oceanic realm

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Radiolarians and conodonts remains have been found from several radiolarite sections in NW-Thailand for which Devonian to Triassic ages are proposed. These new datings allow the establishment of a new stratigraphical scheme and indicate that the geological structure is made of a series of large nappes, similar to those observed in an alpine type orogeny. The position of the suture zone between the Shan-Thai and the Indochina continental blocks is discussed. This suture zone is considered to be the continuation of the Changning-Menglian zones in China. Moreover, these radiolarites are the witness of an oceanic realm which must have been largely open in the Early Devonian and cannot have been closed before the Late Triassic. The size and development speed of this part of the Palaeotethys are tackled. This work shows that the study of radiolarites is an important tool for understanding palaeogeography.

Mid-Coniacian Chalk in the Berkshire Downs: a biostratigraphical problem resolved and a sedimentological enigma recognised

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Lack of preserved macrofossils has long hampered biostratigraphical interpretation of the Mid-Coniacian Upper Chalk succession in the Berkshire Downs. With the recent advent of a more refined lithostratigraphical classification for the Chalk Group, this problem appeared to be resolvable by means of geophysical interpretation. In Sussex, the Mid-Coniacian equates with the Lewes Nodular Chalk / Seaford Chalk boundary, which is coincident with the *M. cortestudinarium* / *M. coranguinum* Zonal boundary, and is also indicated by a marker-bed named Shoreham Marl 2, traceable on geophysical logs.

Integration of new macro- and micropalaeontological data with lithological and geophysical observations demonstrates that, in the Berkshire Downs, the top of the *M. cortestudinarium* Zone

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is in soft, non-nodular chalk, above the geophysical signature previously assumed to represent Shoreham Marl 2. This non-nodular chalk facies has been mapped as Seaford Chalk Formation, but it is coeval with the top of the Lewes Nodular Chalk Formation in the Sussex Basin. As the Berkshire Downs region was a shallow marine shelf during Late Turonian to Mid-Coniacian times, nodular chalk would be expected to be better developed here compared to the Sussex Basin. This was the case in the Late Turonian, but, enigmatically, not in the Mid-Coniacian.

The brachiopod genus *Platystrophia*: return to their original concept

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Platystrophia was established as a genus by King (1850) with *Terebratulites biforatus* Schlotheim (1820) as the type species. The brief original description of *T. biforatus* was based on a single specimen which was not illustrated and was lost by the twentieth century. The type area was determined as south of France. Thus the species name *T. biforatus* can be applied to spirifer-looking taxon from the Palaeozoic or Mesozoic of France, where however there is no indication of the occurrence of *Platystrophia* (*sensu* King). Taxonomic confusion accompanying the name of *T. biforatus* was initiated by Buch (1837), who supposed Baltic "origin" for this species. Consequently, the genus *Platystrophia* is still valid but represents *nomen dubium*. However, the present accepted concept of *Platystrophia* embraces a number of species forming a distinct morphological group. Thus the generic name *Platystrophia* could be saved, but only for the Baltoscandian taxa, as it was proposed originally by King. In particular the type species of the genus can be replaced by *Platystrophia costata* (Pander, 1830) from the late Arenig of St. Petersburg region. The majority of the Late Ordovician North American (Laurentian) species presently referred to *Platystrophia* must be referred to a separate genus because of significant morphological differences from the Baltoscandian taxa.